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THE CLUPEOID FISHES DESCRIBED BY STEINDACHNER

By P. J. P. WHITEHEAD

INTRODUCTION

Most of the new fishes described by Franz Steindachner (1834–1919) are in the Naturhistorisches Museum in Vienna ; a few types and many duplicates are found in other museums. Steindachner's original descriptions and figures are usually excellent, often with far more detail than his contemporaries troubled to include, but modern studies have made a reassessment of his species urgent in certain groups. The opportunity is taken here to redescribe and discuss the types of Steindachner's 21 clupeoid fishes (1 Dussumieriidae, 12 Clupeidae, 8 Engraulidae—see Table 1).

Between 1859 and 1917, Steindachner produced nearly two hundred and fifty papers in which he described about a thousand new species of Recent fishes, 29 fossil species and a number of new reptiles and amphibians. Most of the specimens resulted from his participation in several expeditions, the most important in the present study being those to South America and West Africa.

As a student, Steindachner's legal studies had given way to an interest in natural history (and ichthyology in particular), largely through the encouragement of Eduard Suess. By 1857 Steindachner was a regular visitor to the Imperial natural history cabinet and in 1861 he accepted a permanent post there. One of his first tasks, suggested by Rudolf Kner, was to share with Giovanni Canestrini the study of the material brought back from the Novara Expedition of 1857–9. Determined to enlarge the Imperial collections, Steindachner made expeditions to Switzerland, southern Spain, Portugal and the Canary Islands and in 1868–9 he collected in Senegambia. Subsequently, he accepted Louis Agassiz's invitation to come to Cambridge (Massachusetts) to work on the Thayer material collected in Brazil in 1865–6. Granted leave of absence from Vienna, Steindachner joined Agassiz in March, 1870 and later agreed to accompany him on a collecting trip in the ship *Hassler* on a cruise down the Atlantic coast of the Americas and back up the Pacific coast to San Francisco, a voyage of nine months. For a further seven months Steindachner collected in the United States for the Vienna museum, before returning home.

Twenty-nine years were to elapse before he revisited South America, this time to the northeast provinces of Brazil. In the meantime he participated in and later led three of the Austrian deep-sea Mediterranean expeditions and two Red Sea expeditions, and the fish collections at Vienna grew at such an enormous rate that new accommodation was required. The transfer of the fish and reptile collections from the seven small and dark rooms of the Imperial Cabinet in Joseph Platz to the present museum building was completed by 1886 and the following year Steindachner was

appointed Director of the zoological collections with a suite of rooms which now houses the ichthyological collections. A full account of Steindachner's career has been given by Kähsbauer (1959).

Perusal of the modern fish collection shows to what extent it is indebted to Steindachner's efforts. Amongst the material, there are also Brazilian specimens collected by Johann Natterer (recognizable by red painted roman and arabic numerals on the backs of mounted skins), Japanese fishes (dried) from Burger (many still with paper glued to protect the fins), Red Sea fishes from Eduard Rüppell, type and other material relating to Rudolf Kner and Johann Heckel, and exchange specimens from Leyden, Paris, etc.

Kähsbauer (1959) gave a useful index of the new species described by Steindachner (a few species missing and some MS. names or already published names included).

The Steindachner types are not segregated from the non-typical material and are not always indicated as such ; in some cases a type indication relates merely to a MS. name. No peculiarities of labelling, type of bottle, marking of specimens, etc., were found which would aid in the recognition of types other than the dates given on the labels (which may in some cases refer to the date of incorporation and not to the date of collection).

For the 21 clupeoid species, types were not found for the following species :

Clupea rechingeri (= ? *Herklotsichthys punctatus*)
Clupea notacanthoides (= *Ethmidium maculatum notacanthoides*)
Engraulis nattereri (= *Anchoviella nattereri*)
Engraulis poeyi (= *Lycengraulis poeyi*)

The types of 2 species were reported by Steindachner (see under species) to be in Stuttgart :

Clupea macrolepis (SMNS. 2292)
Clupea neopilchardus (not found, see p. 16).

As an indication of Steindachner's general approach to ichthyology, his clupeoid species can be said to have been described accurately, usually at greater lengths than in contemporary descriptions, but with little or no attempt to explore affinities beyond those of immediate specific relationships. Initially, his clupeoid genera followed those of Valenciennes (1847, 1848), but he later tended to use the two compendium genera, *Clupea* and *Engraulis*, favoured by Günther (1868). Fourteen Steindachner names are here recognized as senior synonyms (Table 1).

The following abbreviations have been used :

S.L.	standard length
tot.l.	total length
g.r.	gillrakers
NMV	Naturhistorisches Museum, Vienna
SMNS	Staatliches Museum für Naturkunde, Stuttgart
BMHN	British Museum (Natural History), London
MNHN	Museum National d'Histoire Naturelle, Paris
RMNH	Rijksmuseum van Natuurlijke Historie, Leyden
ZMA	Zoölogisch Museum, Amsterdam
ZMC	Zoologisk Museum, Copenhagen

I am indebted to Dr. Paul Kähsbauer for his kindly help during my visit to Vienna and for allowing me to borrow many types for further examination.

TABLE 1

Clupeoid species described by Steindachner

Steindachner name	*Identification*
DUSSUMIERIIDAE	
1. *Alausa alburnus* Kner & Steind., 1866	*Spratelloides delicatulus* (Bennett, 1831)
CLUPEIDAE	
2. *Clupea rechingeri* Steind., 1908	? *Herklotsichthys punctatus* (Rüppell, 1837)
3. *Clupea brasiliensis* Steind., 1879	*Sardinella brasiliensis* (Steind., 1879)
4. *Clupea macrolepis* Steind., 1879	*Escualosa thoracata* (Val., 1847)
5. *Clupea amazonica* Steind., 1879	*Rhinosardinia amazonica* (Steind., 1879)
6. *Pellonula bahiensis* Steind., 1879	*Rhinosardinia bahiensis* (Steind., 1879)
7. *Alausa fimbriata* Kner & Steind., 1879	*Sardinops sagax sagax* (Jenyns, 1842)
8. *Clupea neopilchardus* Steind., 1879	*Sardinops sagax neopilchardus* (Steind., 1879)
9. *Clupea setosa* Steind., 1869	*Ethmalosa fimbriata* (Bowdich, 1825)
10. *Clupea notacanthoides* Steind., 1869	*Ethmidium maculatus notacanthoides* (Steind., 1869)
11. *Pellona furthii* Steind., 1875	*Ilisha furthii* (Steind., 1875)
12. *Pellona panamensis* Steind., 1875	*Ilisha furthii* (Steind., 1875)
[*Pellona staudingeri*, MS. name]	*Pellona flavipinnis* (Val., 1837)
[*Pellona macrolepis*, MS. name]	*Pellona flavipinnis* (Val., 1837)
13. *Pristigaster* (*Odontognathus*) *panamensis* Steind., 1876	*Odontognathus panamensis* (Steind., 1876)
ENGRAULIDAE	
14. *Engraulis vaillanti* Steind., 1908	*Anchoviella vaillanti* (Steind., 1908)
15. *Engraulis nattereri* Steind., 1879	*Anchoviella nattereri* (Steind., 1879)
16. *Engraulis januaria* Steind., 1879	*Anchoa januaria* (Steind., 1879)
17. *Engraulis nasus* Kner & Steind., 1866	*Anchoa nasus* (Kner & Steind., 1866)
18. *Engraulis peruanus* Steind., 1879	*Anchoa nasus* (Kner & Steind., 1866)
19. *Engraulis panamensis* Steind., 1875	*Anchoa panamensis* (Steind., 1875)
20. *Engraulis macropolepidotus* Kner & Steind., 1865	*Anchovia macrolepidota* (Kner & Steind., 1865)
21. *Engraulis poeyi* Kner & Steind., 1865	*Lycengraulis poeyi* (Kner & Steind., 1865)

Family **DUSSUMIERIIDAE**
SPRATELLOIDES Bleeker, 1851

Spratelloides Bleeker, 1851, *Natuurk. Tijdschr. Ned. Ind.*, **2** : 214 (Type : *Clupea argyrotaeniata* Bleeker = *Clupea gracilis* Temminck & Schlegel).

In a recent revision of the genus (Whitehead, 1962) two species were recognized, *S. gracilis* (Temm. & Schl.) and *S. delicatulus* (Bennett). Subsequent studies have dealt with type specimens (Whitehead *et alii*, 1966 : 33–37), further differences between the two species (Whitehead, 1965 : figs. 2, 3; supra-maxillary shape, posterior frontal fontanelles) and distribution (Whitehead, 1969a).

1. *Alausa alburnus* Kner & Steind., 1866
= *Spratelloides delicatulus* (Bennett, 1831)

(Plate 1a)

Clupea delicatula Bennett, 1831, *Proc. zool. Soc. London*, **1** : 168 (Mauritius).
Alausa alburnus Kner & Steindachner, 1866, *Sitzb. K. Akad. Wiss. Wien*, **54** : 387, pl. 1, fig. 16 (" Valparaiso "—in fact Samoa, see below).

LOCALITY. As pointed out by Günther (1909 : 384), the original reference number and the locality recorded for this species by Schmeltz (1869 : 25) in the catalogue of the Godeffroy Museum at Hamburg were attributed by Kner & Steindachner to *Alausa fimbriata*, and *vice versa*. The correct locality for *Alausa alburnus* is thus Samoa ; *Stolephorus delicatulus* is not recorded from the Pacific coasts of America.

TYPE MATERIAL. a. LECTOTYPE, a fish of 43·0 mm S.L. *ex* Godeffroy Museum Reg. No. 2152, from Samoa in 1866, NMV.4282.

b. PARALECTOTYPE, a fish of 40·8 mm S.L. (source as above).

There are two further specimens, 49·1.–51·5 mm S.L. *ex* Godeffroy Museum, from Samoa in 1869, NMV.4328 (locality correctly stated as Samoa on label).

DESCRIPTION. A fish, 43·0 mm S.L., LECTOTYPE, *ex* Samoa ; in fair condition but dorsal and anal fins slightly damaged and caudal lobes broken, NMV.4283.

Br.St. ?, D ii 8, P i 11, V i 7, A ii 8, g.r. 30.

In percentages of standard length : body depth 18·8, body width 9·1, head length 25·6 ; snout length 7·0, eye diameter 7·4, length of upper jaw 9·3, length of lower jaw 10·7 ; pectoral fin length 12·6, pelvic fin length 10·9, length of anal base 8·1 ; pre-dorsal distance 47·5, pre-pelvic distance 56·5, pre-anal distance 79·5.

Body a little compressed, its width twice in depth, belly rounded and without scutes except for W-shaped pre-pelvic scute ; head longer than body depth ; eye diameter a little greater than snout length. Upper jaw reaching to anterior eye border ; pre-maxillae triangular, toothless ; maxillae toothless ; two supra-maxillae, the 1st (anterior) plate-like and attached to upper edge of maxilla, the 2nd (posterior) supra-maxilla with slender anterior shaft and expanded posterior part, the latter as deep as long (about 1·0 mm), its upper profile rising steeply, its lower profile joining anterior shaft opposite that of upper profile (as in *Sardinella* ; cf. the more asymmetrical shape in *Harengula*). Lower jaw about twice as long as deep, highest point in first third of length ; articulation of lower jaw below vertical from anterior pupil border.

Posterior border of operculum with slight indentation in upper part ; lower border of operculum horizontal. Cleithrum with well developed fleshy cleithral lobes. Isthmus silvery, sterno-hyoideus muscle ending abruptly anteriorly, the urohyal exposed in front of this until concealed by gill membrane. Gillrakers long, slender, about $\frac{1}{2}$ eye diameter, lined with 20–25 fine serrae on each side ; about 6 short gillrakers on posterior face of 3rd epibranchial ; gill filaments about $\frac{2}{3}$ length of gillrakers. Pseudobranch present, exposed, about $\frac{7}{8}$ eye diameter. Dorsal surface of head without striae, posterior frontal fontanelles together almost circular, 0·9 mm long (equal to pupil), anterior extension of supra-occipital slender.

Dorsal fin origin nearer to snout tip than to caudal base by just over 1 eye diameter. Pectoral fin tips fail to reach pelvic base by 2¼ eye diameters. Pelvic fin base under 8th branched dorsal ray, nearer to anal origin than to pectoral base by ⅔ eye diameter. Anal fin origin nearer to caudal base than to pelvic base by ⅔ eye diameter.

Unexposed portion of scales with one main and 2 (anterior) to 4 (posterior) subsidiary complete vertical striae ; exposed portion of scale without crenulations, striae or perforations.

Colour : upper ¼ brown, remainder silvery ; no silvery lateral stripe.

IDENTIFICATION. The absence of a silver lateral stripe (Whitehead, 1962 : 338) and the shape of the posterior frontal fontanelles and posterior supra-maxilla (Whitehead, 1965 : figs. 2, 3), clearly identify the present specimen as *Spratelloides delicatulus*. The smaller pectoral fins place it in the nominate subspecies (Whitehead, 1962 : 347), which is consistent with its presumed provenance (Samoa).

Fowler (1941 : 565) recognized *Alausa alburnus* as a distinct species, but Bertin (1943) and Schultz & Wellander (1953) correctly placed it in the synonymy of *S. delicatulus*.

Family **CLUPEIDAE**

HERKLOTSICHTHYS Whitley, 1951

Herklotsichthys Whitley, 1951, *Proc. Roy. zool. Soc. N.S.W.*, 1949–50 : 67 (Type : *Harengula dispilonotus* Bleeker).

A single Steindachner species, *Clupea rechingeri*, is rather doubtfully included in this Indo-Pacific genus.

2. ***Clupea rechingeri*** Steindachner, 1908
= ***?Herklotsichthys punctatus*** (Rüppell, 1837)

Clupea punctata Rüppell, 1837, *Neue Wirbelth., Fische* : 78, pl. 21 (2) (Red Sea).
Clupea rechingeri Steindachner, 1908, *Sitzb. K. Akad. Wiss. Wien*, **115** (1) : 1424 (Upolu, Samoa).

TYPE MATERIAL. The two specimens described by Steindachner (no size given) cannot now be found.

IDENTIFICATION. The criteria now used to distinguish the genera *Sardinella* and *Herklotsichthys* (Whitehead, 1964a) do not appear in the description of *C. rechingeri* and Steindachner gave no clue to its relationship to other species. Regan (1917 : 392) and Fowler (1941 : 597) identified *Clupea rechingeri* with *Harengula vittata* (= *Sardinella melanura* (Cuvier) *fide* Whitehead, 1967a : 66). The latter has very distinctive black caudal tips (retained in alcohol specimens), whereas Steindachner's description seems to allude to the general darkening of the whole caudal margin found in many species of *Herklotsichthys* and *Sardinella* : *Die Spitzen der Schwanzflossen lappen und der Innenrand derselben sind dunkel angeflogen. Herklotsichthys punctatus* is one of the commonest Indo-Pacific clupeids and Steindachner's description fits the species.

SARDINELLA Valenciennes, 1847

Sardinella Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 261 (Type : *Sardinella aurita* Valenciennes).

As yet, there is no modern world-wide study of the *Sardinella* species with 9 pelvic finrays (*S. aurita, S. longiceps, S. anchovia, S. brasiliensis*). In the Indo-Pacific region, *S. aurita* and *S. longiceps* (whose ranges apparently do not overlap) can be easily distinguished (Chan, 1965), but studies of *aurita*-like fishes in the Atlantic have not compared Eastern with Western Atlantic forms, or both with the Western Pacific *S. aurita*, at least on the basis of adequate material.

3. ***Clupea brasiliensis*** Steindachner, 1879
= ***Sardinella brasiliensis*** (Steindachner, 1879)

Clupea brasiliensis Steindachner, 1879, *Sitzb. K. Akad. Wiss. Wien*, **80** : 182 (fish market, Rio de Janeiro) (*non Clupea brasiliensis* Schneider, 1801 = *Albula vulpes*—the Schneider name now a *nomen oblitum*) ; Idem, 1880, *Ichthyol. Beitr.*, **8** : 64.

Clupea janeiro Eigenmann & Bray, 1894, *Ann. N.Y. Acad. nat. Sci.* : 626 (replacement name for the preoccupied *Clupea brasiliensis* Steindachner).

Synonymy. *Clupea brasiliensis* Steindachner (a species of *Sardinella*) is a primary homonym of *Clupea brasiliensis* Schneider (= *Albula vulpes*—Whitehead, 1969b). Fowler (1941 : 602) avoided the issue by resurrecting the earlier Rafinesque name *allecia* for the *Sardinella* species, but this name is both doubtfully legal (Whitehead, 1967a : 40) and applies to the Mediterranean species of *Sardinella* ; as shown below, Steindachner's Brazilian species is possibly distinct. Myers (in Rivas, 1964 : 410) believed that a new name was required for the latter, but overlooked *Clupea janeiro* of Eigenmann and Bray. The Schneider name has not been used, however, as a senior synonym for over fifty years (see full synonymies in Fowler, 1941 and Hildebrand, 1964) and it thus qualifies as a *nomen oblitum* under Article 23(b) of the International Code. Application will be made to place the Schneider name on the Official Index and thus to release the Steindachner name for this species of *Sardinella*.

Type material

a. LECTOTYPE, a fish of 143·3 mm S.L., *ex* Rio de Janeiro in 1877, NMV.1156 (jar labelled VII 126 n.sp.).
b. PARALECTOTYPES, 2 fishes, 121·0–121·2 mm S.L., *ex* Rio de Janeiro in 1874, NMV.1158 (jar labelled I 13 . . .).
c. PARALECTOTYPES, 2 fishes, 114·4–140·7 mm S.L., *ex* Rio de Janeiro in 1874, NMV.1159 (jar labelled I 1356 pt.b).
d. PARALECTOTYPES, 4 fishes, 116·7–120·7 mm S.L., *ex* Rio de Janeiro in 1874, NMV.1160 (jar labelled I 1216a).
e. PARALECTOTYPE, 1 fish, 120·5 mm S.L., *ex* Rio de Janeiro, in 1874, NMV. 1161 (jar labelled I 1623).
f. PARALECTOTYPES, 4 fishes, 114·0–121·7 mm S.L., *ex* Rio de Janeiro in 1874, NMV.1162 (jar labelled I 1216 pt.).

g. ? PARALECTOTYPE, 1 fish, 148·3 mm S.L., *ex* Rio de Janeiro in 1879, NMV. 1155 (jar labelled coll. Pape 62). This fish may not have been available when the original description was made.

Description. A fish, 143·3 mm S.L., 180 mm tot.l. (estimated, caudal tips damaged), LECTOTYPE, *ex* Rio de Janeiro fish market in 1874, in good condition except caudal, NMV.1156.

Br.St. 6, D v 14, P i 15, V i 8, A iii 15, g.r. 155, scutes 19+14.

In percentages of standard length : body depth 22·5, body width 12·4, head length 27·7 ; snout length 7·5, eye diameter 6·6, length of upper jaw 11·0, length of lower jaw 13·9, height of lower jaw 6·0, sub-ocular depth 7·3, least post-orbital distance 11·9 ; pectoral fin length 16·9, pelvic fin length 9·7, length of anal base 12·8 ; pre-dorsal distance 45·5, pre-pelvic distance 52·7, pre-anal distance 79·2.

Body a little compressed, its width 1⅘ in depth, belly rounded before pelvic base but scutes more keeled behind ; head length greater than body depth, post-orbital portion a little less than ½ length of head. Snout a little longer than eye diameter. Upper jaw toothless, reaching to vertical from eye centre ; two supra-maxillae, the posterior with slender anterior shaft and lozenge-shaped expanded portion posteriorly, its upper and lower profiles meeting anterior shaft at the same point. Lower jaw toothless, rising steeply anteriorly, its height 2⅓ times in its length, its articulation slightly behind vertical from eye centre. Fine granular teeth present on tongue, palatines and ectopterygoids.

Posterior border of operculum with slight indentation in its upper part, lower border horizontal ; sub-operculum rectangular but posterior angle evenly rounded ; inter-operculum about ⅓ eye diameter at widest point. Posterior border of gill opening with two fleshy lobes ; cleithral lobe present ; isthmus slender, tapering, the sterno-hyoideus muscle extending forward to gill membrane. Gillrakers fine and slender, the longest 8·9 mm (a little more than eye diameter) ; mediopharyngobranchial present, its length ⅔ eye diameter, bearing the first thirty upper gillrakers ; over one hundred slender gillrakers present on posterior face of 3rd epibranchial ; gill filaments of anterior hemibranch on first arch ½ eye diameter and ¾ length of those of posterior hemibranch. Pseudobranch present, exposed, extending onto inner face of operculum, equal to eye diameter, with 20 filaments ; ventral border forming a distinct ridge with a longitudinal groove below for reception of tips of hypobranchial rakers of first arch. Fronto-parietal region of head with two cuneiform areas bearing about ten longitudinal striae, a well-defined transverse ridge on the supra-occipital and several smaller striae above the eyes.

Dorsal fin origin nearer to snout tip than to caudal base by 1⅔ eye diameters ; base of fin invested in low scaly sheath. Pectoral fin tips fail to reach pelvic base by 1⅓ eye diameters ; no axillary scale but a groove above first unbranched ray for reception of fin. Pelvic fin base nearer to pectoral base than to anal origin ; axillary scale present, ¾ length of fin. Anal fin origin nearer to caudal base than to pelvic base by ½ eye diameter ; base of fin invested in low scaly sheath, final anal ray much branched and about twice length of antepenultimate ray.

Unexposed portion of scales with one continuous and 2 (anterior) to 4 (posterior)

minor vertical striae, the later broken in centre of scale (except for posterior striation in some post-dorsal scales) ; exposed border of scale with fine crenulations and faint horizontal lines.

Colour : upper ¼ of body brown, remainder silvery ; small dark semicircular area on posterior border of operculum due to absence of guanine layer on inner face ; faint dark tips to dorsal branched rays.

IDENTIFICATION. Regan (1917 : 378) placed *Clupea brasiliensis* Steindachner in the synonymy of the widespread *Sardinella aurita* Valenciennes, but Longley & Hildebrand (1941) noticed higher gillraker counts in three out of four syntypes of *Sardinella anchovia* Valenciennes (= *S. aurita*) and recognized these three specimens as distinct and most likely Steindachner's *brasiliensis*. Hildebrand (1964 : 399) separated *S. brasiliensis* from the two other Western Atlantic species, chiefly on the basis of its higher gillraker count (numbers increase in larger fishes, however), which he cited as :

S. brasiliensis	110–130 (160–178 in Longley & Hildebrand, 1941)
S. pinnula Bean	75–80
S. anchovia	55–100

The three doubtful syntypes of *S. anchovia* (104·5–143·6 mm S.L.) have been re-examined (Whitehead, 1967a : 42) and their high gillraker count was confirmed (151, 174, 179). Another difference between these *brasiliensis*-like syntypes and the remaining true lectotype of *S. anchovia* was found to be the greater depth of the cheek in the former (greater than vertical eye diameter). On the basis of gillraker counts and cheek depth it was accepted that *S. brasiliensis* differed from other Western Atlantic species and probably also from *S. aurita* of the Mediterranean, Eastern Atlantic and Pacific (which is also most likely one of the Western Atlantic species, i.e. the *S. anchovia* of authors—see Whitehead, 1967a : 43).

Examination of specimens of *S. aurita* from the Mediterranean, West Africa and the Philippines has now shown, however, that *S. brasiliensis* cannot be separated from them on its apparently deeper cheek. Furthermore, the total range in gillraker numbers (66–166 *fide* Chan, 1965 ; up to 280 in 350 mm fishes *fide* Rossignol, 1955) means that separation will depend on a formula relating gillraker counts to length of fish. Lima (1966) described as *S. brasiliensis* six specimens of 128–160 mm S.L. from Estado do Ceará, Brazil. Her gillraker counts of 64–128, however, appear to be too low for fishes of this size, at least as far as the figures for the types of *brasiliensis* are concerned ; on the other hand, they are close to the numbers cited by Hildebrand (1964). The identify of *S. brasiliensis* must depend, therefore, on examination of large samples, especially from the Western Atlantic. Descriptions of the types of *brasiliensis*, *anchovia* and *aurita* reveal only small differences which, although not totally vindicating Regan's synonymizing of the three, at least suggest that no Western Atlantic study can afford to ignore the Eastern Atlantic, Mediterranean and Pacific forms of *S. aurita*.

ESCUALOSA Whitley, 1940

Escualosa Whitley, 1940, *Aust. Zool.*, **9** (4) : 402 (Type : *Clupea macrolepis* Steindachner = *Kowala thoracata* Valenciennes).

Generic and species synonymies are discussed in Whitehead (1964a ; 1967a : 70) and Whitehead *et al.* (1966 : 70) and a key to this section of the Clupeinae appears in Whitehead (1968).

4. *Clupea macrolepis* Steindachner, 1879 = *Escualosa thoracata* (Valenciennes, 1847)

Kowala thoracata Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 363 (Pondicherry ; type redescribed in Whitehead, 1967a).

Clupea macrolepis Steindachner, 1879, *Denkschr. Akad. Wiss. Wien*, **41** (2) : 13 (Townsville, Queensland ; type of *Escualosa* Whitley, 1940).

TYPE MATERIAL. HOLOTYPE, a fish of 64 mm S.L., *ex* Townsville, Cleveland Bay, Queensland, Australia, coll. Baron Ferdinand von Müller, SMNS.2292.

DESCRIPTION. Proportional and meristic characters for the holotype were given in Whitehead (1964a : 44, Table III). In all respects the type conforms to the more detailed description of the species given in the same publication (p. 45) and in Whitehead (1967a : 71).

SYNONYMY. *Clupea macrolepis* Steindachner has been shown to be a junior synonym of *Kowala thoracata* Valenciennes (Whitehead, 1964a : 43). Whitley (1940 : 402) designated *Clupea macrolepis* type of *Escualosa* Whitley. Since *Leptogaster* Bleeker proved to be a *nomen oblitum* (Whitehead *et alii*, 1966 : 70) and *Kowala* Valenciennes a synonym of *Sardinella* (Whitehead, 1964a : 52), the genus *Escualosa* was recognized, containing the single species *E. thoracata*. Whitley (1940 : fig. 9) figured a specimen of *Harengula* sp. and suggested that it represented the adult of his *Escualosa macrolepis*. The following year (Whitley, 1941 : 1) he found in Paris a replacement specimen of the type of *Harengula abbreviata* Valenciennes (the real type being missing), identifying it as *Kowala castelnaui* Ogilby " whose name is obviously a synonym of *abbreviata* which belongs to my genus *Escualosa*, 1940 ". In fact, the replacement specimen does not match the description of *abbreviata* and the latter name should be considered a *nomen dubium* (Whitehead, 1967a : 69). Whitley's specimen of *Harengula* appears to be *Herklotsichthys castelnaui* and *Escualosa* remains a monotypic genus distinguished by possession of 7 pelvic rays, a silver lateral stripe and a large rectangular 2nd supra-maxilla (see key, Whitehead, 1968 : 478).

RHINOSARDINIA Eigenmann, 1912

Heringia Fowler, 1911, *Proc. Acad. nat. Sci. Philad.*, **63** : 207 (Type : *Clupea amazonica* Steindachner) (name preoccupied in Diptera—Myers, 1929, *Copeia* : 1).

Rhinosardinia Eigenmann, 1912, *Mem. Carnegie Mus.*, **5** : 445 (Type : *Rhinosardinia serrata* Eigenmann = *R. amazonica* Steindachner).

The curious retrorse spine at the anterior end of the maxilla sets this genus apart from all others (see key in Whitehead, 1968 : 478). A small projection occurs in

Escualosa (Whitehead, 1964a : fig. 2c) but this is blunt and points upwards and not backwards. In other respects *Rhinosardinia* is very similar to the South American genera *Lile* and *Ramnogaster*. Regan (1917 : 394) placed *Rhinosardinia* (as *Heringia*) with *Lile*, *Sardinella* and *Harengula*, i.e. in the Clupeinae. Hildebrand (1964 : 261) allied *Rhinosardinia* with the Pristigasterinae, but current definitions of the clupeid subfamilies (e.g. Whitehead *et alii*, 1966 : 37), although by no means satisfactory, exclude *Rhinosardinia* from the Pristigasterinae, because of its short anal fin (under 20 rays ; cf. over 30), and place it in the Clupeinae.

At species level, the South American clupeids show rather little relationship to the West African or Indo-Pacific clupeids (only *Sardinella aurita* is found on both sides of the Atlantic), and only the genera *Sardinella*, *Ilisha* and *Pellona* are shared (the last not from West Africa). It has been argued, therefore (Whitehead, 1968), that the South American Clupeinae have evolved in isolation. The similarities between *Rhinosardinia* and the Indo-Pacific *Escualosa* may thus be coincidental, resulting from relatively limited variations possible within the clupeine framework.

In *Escualosa*, as also in *Rhinosardinia* (but less so in *R. bahiensis*) the upper jaw is more or less notched, a condition typical of the shads (subfamily Alosinae). Although *Brevoortia*, *Ethmidium*, *Ethmalosa* and the Indo-Pacific shads (*Hilsa*, *Gudusia*) have very long and numerous gillrakers and no jaw teeth, teeth and short, sparse rakers are found in some species of *Alosa* (*sensu* Svetovidov, 1964, i.e. including *Pomolobus* and *Caspialosa*). Future work may show that *Rhinosardinia* can be derived as convincingly from the *Alosa* stem as from the Western Atlantic Clupeinae.

5. ***Clupea amazonica*** Steindachner, 1879
= ***Rhinosardinia amazonica*** (Steindachner, 1879)

Clupea amazonica Steindachner, 1879, *Sitzb. K. Akad. Wiss. Wien*, **80** : 183 (Amazon R. at Pará ; 4 fishes, 40–75 mm tot. l.) ; *Idem*, 1880, *Ichthyol. Beitr.*, No. 8 : 65 (repeat).
Rhinosardinia serrata Eigenmann, 1912, *Mem. Carnegie Mus.*, **5** : 445, text fig. 39, pl. 62 (figs. 3 and 4) (*ex* Morawhanna and Mora Passage, British Guiana).

TYPE MATERIAL. a. LECTOTYPE, a fish of 54·8 mm S.L. (74·0 mm tot.l.), *ex* Pará, Amazon River in 1879, NMV.1104.

b. PARALECTOTYPES, 3 fishes 31·2–42·2 mm S.L. from the same jar.

Steindachner listed only 4 fishes. A fifth specimen in this jar (25·9 mm S.L., 32 mm tot.l.) is too small to have been part of the original description.

DESCRIPTION. A fish 54·8 mm S.L. (74·0 mm tot.l.) *ex* Pará, Amazon River, in good condition, NMV.1104.

Br.St. 5 (left 6), D ii 13, P i 11, V i 7 (both sides), A iii 13, g.r. 38, scutes 17+11.

In percentages of standard length : body depth 30·3, head length 24·1 ; snout length 5·75, eye diameter 7·3, length of upper jaw 9·85, length of lower jaw 9·5, depth of lower jaw 5·6 ; pectoral fin length 19·8, pelvic fin length 12·4, length of anal fin base 13·0, length of dorsal base 14·2, height of dorsal fin 18·6 ; pre-dorsal distance 51·0, pre-pelvic distance 51·0, pre-anal distance 76·5 ; depth of caudal peduncle 13·3.

Body compressed, belly with trenchant keel of scutes, body depth greater than head length. Snout shorter than eye diameter. Upper jaw with two supra-maxillae,

the 1st (anterior) slender, the 2nd (posterior) with diamond shaped expanded portion reaching to posterior tip of maxilla ; minute teeth present on lower edge of maxilla below centre of 2nd supra-maxilla, and a sharp retrorse spine (= to half pupil diameter) on upper edge of maxilla in front of anterior supra-maxilla ; upper jaw with a slight median notch. Lower jaw profile rising steeply, its deepest part in first $\frac{1}{3}$ of its length, the jaw 1·6 times as long as deep. No teeth on pre-maxillae or lower jaw or within mouth.

Gillrakers fine and slender, $\frac{1}{2}$ eye diameter and a little longer than corresponding gill filaments ; about 10 short rakers on posterior face of 3rd epibranchial. Pseudobranch $\frac{3}{4}$ eye diameter, with 11 filaments. Operculum with anterior and posterior margins parallel, the lower border rising at about 40° ; sub-operculum rectangular with rounded posterior border ; inter-operculum deep posteriorly, tapering evenly to the lower jaw articulation. Fronto-parietal region of head smooth, posterior frontal fontanelles occluded.

Dorsal fin origin midway between tip of snout and base of caudal fin ; dorsal height (last unbranched ray) 1·30 times length of dorsal base. Pectoral fin failing to reach pelvic base by just over 1 eye diameter ; no axillary scale present. Pelvic fin base in advance of dorsal origin by almost 1 pupil diameter and equidistant between pectoral base and anal origin ; axillary scale present, $\frac{1}{3}$ length of fin. Anal origin equidistant between pelvic base and base of caudal fin. Depth of caudal peduncle 2·27 times in body depth.

Unexposed portion of scales with one continuous vertical striation and up to three small radiating striae not reaching to centre of scale ; exposed portion of scale with two horizontal striae converging to centre of scale. Small scales present on caudal.

Colour : overall brownish, but with no suggestion of a silver lateral stripe (absent also in paralectotypes).

Synonymy. Regan (1917 : 394) considered *R. serrata* Eigenmann a synonym of *R. amazonica*, but Hildebrand (1964 : 415) after " careful rereading of the original description of *amazonica* " decided to separate the two on small differences in body

	R. amazonica (LECTOTYPE) NMV.1104	*R. serrata* (SYNTYPE) USNM.66284	*R. serrata* (4 SYNTYPES) BMNH.1911.10. 31.452–5
S.L.	54·8	47·3	44·5–49·6
As % of S.L.			
Body depth	30·3	30·0	28·5–30·5
Head length	24·1	23·8	21·6–23·3
Caudal peduncle depth	13·3	13·1	12·7–13·5
Dorsal fin :			
base	14·2	12·7	12·2–13·8
height	18·6	18·0	18·7–20·0
$\frac{\text{height}}{\text{base}}$	1·31	1·42	1·43–1·49
$\frac{\text{Body depth}}{\text{Caudal ped. l.}}$	2·27	2·29	2·18–2·31
Gillrakers	38	35	33, 34, 34, 35

depth, depth of caudal peduncle, head and snout length and length of dorsal fin base. A comparison between five syntypes of *R. serrata* and the lectotype of *R. amazonica* does not bear out Hildebrand's distinction between these two nominal species.

The slightly longer dorsal fin base in the lectotype of *R. amazonica* and its slightly higher gillraker count hardly justify separation of the two species. The range of *R. amazonica* thus extends from the mouth of the Amazon, through the Guianas to the San Juan river in Venezuela.

6. ***Pellonula bahiensis*** Steindachner, 1879
= ***Rhinosardinia bahiensis*** (Steindachner, 1879)

(Plate 1b)

Pellonula bahiensis Steindachner, 1879, *Sitzb. K. Akad. Wiss. Wien*, **80** : 181, pl. 3 (fig. 2) (*ex* Bahia, 8 fishes to 100 mm tot.l.) ; *Idem*, 1880, *Ichthyol. Beitr.*, No. 8 : 63, pl. 3 (fig. 2) (repeat).

TYPE MATERIAL. LECTOTYPE, a fish of 69·1 mm S.L. (90·5 mm tot.l.), in good condition but some scales missing, *ex* Bahia in 1879, NMV.2870.

PARALECTOTYPE, a fish of 70·5 mm S.L. from the same bottle.

DESCRIPTION. A fish, 69·1 mm S.L. (90·5 mm tot.l.), LECTOTYPE, *ex* Bahia, NMV.2870.

Br.St. 6 (6 right), D iii 15, P i 13, V i 7, A iii 14, g.r. 32, scutes 17+11.

In percentages of standard length : body depth 27·3, body width 11·1, head length 25·0 ; snout length 6·4, eye diameter 8·7, length of upper jaw 11·9, length of lower jaw 11·9, depth of lower jaw 6·2 ; pectoral fin length 15·9 pelvic fin length 12·7, length of dorsal fin base 17·5, height of dorsal fin 19·0, length of anal fin base 16·2 ; pre-dorsal distance 46·1, pre-pelvic distance 49·8, pre-anal distance 72·5.

Body compressed, its width 2½ times in its depth, belly keeled, scutes with long sharp spines partly concealed by scales on either side of midline ; head a little shorter than body depth. Snout a little shorter than eye diameter. Upper jaw reaching almost to vertical from eye centre ; two supra-maxillae, the 1st (anterior) long and plate-like, the 2nd (posterior) of typical *Harengula* shape and reaching to posterior tip of jaw ; maxilla with a small blunt projection (? damaged ; = retrorse spine in paralectotype) on upper face of maxilla in front of 1st supra-maxilla ; minute denticulations along lower edge of maxilla below 2nd supra-maxilla ; upper jaw without marked notch. Lower jaw profile rising steeply, its deepest part in first ⅓ of its length, the jaw 1·91 times as long as deep. Small conical teeth present at dentary symphysis (left 4, right 3), on pre-maxillae (left 4, right 7) and even smaller on palatines and ecto-pterygoids.

Gillrakers fine and slender, the longest just under half eye diameter, 1¼ times length of corresponding gill filaments ; seven short triangular rakers present on posterior face of third epibranchial ; short mediopharyngobranchial present, bearing 6 gillrakers. Pseudobranch present, exposed, ⅔ eye diameter, with 14–15 filaments. Cleithral lobe present. Exposed portion of inter-operculum a narrow crescent, less than half depth of sub-operculum. Frontals diverging in the midline posteriorly to expose a triangle of the supra-occipital ; posterior frontal fontanelles not exposed ;

fronto-parietal region with a series of short longitudinal striae (not as strongly developed, however, as in e.g. *Sardinella*).

Dorsal fin origin nearer to snout than to caudal by just over 1 eye diameter and in advance of vertical from pelvic base by 1 pupil diameter ; base of fin 1·09 times in its height. Pectoral fin tips failing to reach pelvic base by just over 1 eye diameter ; axillary scale absent (apparently) but a short groove present above proximal ⅓ of first ray. Pelvic fin base nearer to pectoral base than to anal origin by ½ pupil diameter ; axillary scale present, a little over ½ length of fin. Anal fin origin about equidistant between pelvic and caudal bases ; a low sheath of scales along base of fin.

Scales : unexposed portion of scale with one major and up to three minor striae, the former vertical and continuous across scale, the latter radial and only occasionally traversing scale ; exposed portion of scale without striae or with one or two very short radial striae.

Colour : body brown, with very distinct silver lateral band from opercular opening to caudal base, almost as broad as eye ; opercular series and belly silvery.

NOTE. Regan (1917 : 395) doubted that *Pellonula bahiensis* could be separated from *Clupea amazonica* on the basis of its silver lateral stripe, since specimens of the latter " also show a faint lateral band in certain lights. " The stripe in *R. bahiensis* is, however, quite as distinct as that which separates e.g. *Spratelloides gracilis* from *S. delicatulus* in all except post-larval size groups. It was well illustrated by Steindachner (see Plate 1b).

Rhinosardinia amazonica and *R. bahiensis* were clearly distinguished by Hildebrand (1964 : 411), but examination of the types necessitates some modifications to the key (as stated earlier, *R. serrata* is a synonym of *R. amazonica*).

KEY TO SPECIES ***Rhinosardinia***

1 Silver lateral stripe present ; exposed portion of scales without 2 prominent horizontal striae ; dorsal fin origin nearer to snout than to caudal base by 1 eye diameter ; inter-operculum visible as narrow crescent, ½ as deep as sub-operculum . . ***Rhinosardinia bahiensis*** (Steind.)

2 No silver lateral stripe ; exposed portion of scales with 2 prominent horizontal striae ; dorsal fin origin equidistant between snout tip and caudal base ; inter-operculum broadly exposed, at its widest as deep as sub-operculum . . . ***Rhinosardinia amazonica*** (Steind.)

SARDINOPS Hubbs, 1929

Sardinops Hubbs, 1929, *Proc. Calif. Acad. Sci.*, **18** (11) : 264 (Type : *Meletta caerulea* Girard).

As in other wide-ranging genera with a discontinuous distribution, the various forms of *Sardinops* have sometimes been considered to be distinct species and sometimes merely subspecies. Regan (1916 : 14) and Chabanaud (1926) suspected the latter but excluded *S. neopilchardus* of Australia and New Zealand ; Svetovidov (1952 : 177) recognized five subspecies of *Sardinops sagax*, but with some reservation regarding *neopilchardus*, in which the head is longer, the maxilla shorter and the gillrakers less numerous than in the other forms. On present evidence, Svetovidov's solution seems best.

7. *Alausa fimbriata* Kner & Steindachner, 1866
= *Sardinops sagax sagax* (Jenyns, 1842)

(Plate 1c)

Clupea sagax Jenyns, 1842, *Zool. Beagle, Fish.* : 134 (*ex* San Lorenzo I., Lima).
Alausa fimbriata Kner & Steindachner, 1866, *Sitzb. K. Akad. Wiss. Wien*, **54** : 386, pl. 15 (" Valparaiso? ", no size, from Museum Godeffroy).

Locality. As noted earlier (p. 6), Steindachner confused the reference number and locality of this species with that of his *Alausa alburnus*. The correct locality is thus Valparaiso, Chile.

Type material. Intensive search produced no specimen labelled *Alausa fimbriata* in Vienna. But Steindachner's description and figure are quite sufficient to identify this species and provision of a neotype would serve no useful purpose.

Identification. Steindachner's pl. 15 (shown here, Plate 1c) shows the striations on the operculum, the enlarged anal rays and the large alar scales that characterize members of *Sardinops* ; the description is quite consistent with this identification. A series of black spots often occurs along the flank but this was apparently not the case in Steindachner's specimen.

Steindachner appears to have been unaware of Jenyns work on the *Beagle* collection.

8. *Clupea neopilchardus* Steindachner, 1879
= *Sardinops sagax neopilchardus* (Steindachner, 1879)

Clupea lata Richardson, 1843, *Trav. N.Z.* (Dieffenbach), **2** : 221 (on Solander MS. name *Clupea lata—nomen nudum*).
Clupea neopilchardus Steindachner, 1879, *Denkschr. Akad. Wiss. Wien*, **41** : 12 (not quite 170 mm, *ex* Hobson's Bay, Victoria, type in Stuttgart Museum).

Type material. The type is apparently no longer present in Stuttgart. This sub-species is sufficiently well defined geographically (southern Australia and New Zealand—nearest related forms in South Africa and along Pacific coast of South America) for the provision of a neotype to be unnecessary at the present time, particularly in view of the excellent study of the Australian form by Blackburn (1949).

Richardson's *Clupea lata* is not accompanied by any description but merely a reference to Solander's MS. description in his notebook (*Pisces Australiae*, p. 17) made during Captain Cook's first voyage to the Pacific. Solander's description reads :

> *Clupea lata* B.18
> Habitat Tolaga
> Argentea, nitidipinna ; Dorso e cinereo caeruleo nitente, ut et superna pars capitis.
> *Pinna analis* basi plumbea, alias omnes colore corporis ubi sita.
> *Pinna caudalis* tota plumbea
> Iris argentea, superne semper nebula nigra.

This description is not adequate to identify the species and no drawing of *Clupea lata* was made by Sydney Parkinson, the artist on this voyage. The name *Clupea lata* is a *nomen nudum.*

9. ***Clupea setosa*** Steindachner, 1869
= ***Ethmalosa fimbriata*** (Bowdich, 1825)
(Plate 2a)

Clupea fimbriata Bowdich, 1825, *Excurs. Madeira* : 234, fig. 44 (Porto Praya, Cape Verde Is.—probably the Gambia *fide* Whitehead, 1967b : 590).

Clupea setosa Steindachner, 1869, *Sitzb. K. Akad. Wiss. Wien,* **60** : 311, pl. 6 (*ex* Mazatlan stated —in fact West Africa) ; *Idem,* 1869, *Ichthyol. Notizen,* No. 9 : 22, pl. 6 (repeat).

Locality. Steindachner (1882 : 14) subsequently realized that his specimens had not come from Mazatlan (Mexico) but were from the coasts of Liberia and Gabon, West Africa.

Type material. LECTOTYPE, a fish of 184·0 mm S.L. (253·0 mm tot.l.), *ex* West Africa (Liberia or Gabon coasts), NMV.4173.

PARALECTOTYPES, two fishes, 174·5–178·0 mm S.L., as above, caudal lobes damaged.

The specimens are accompanied by labels reading :

" *Coll. Musei Vindobonensis* 4173
CLUPEA altata Std. ALTATA Steind. 1878 I 20 "

and

" *Coll. Musei Vindobonensis* 4173
CLUPEA setosa Steind. ALTATA (Mexico Sinaloa) 1878 ".

Description. A fish, 184·0 mm S.L. (253·0 mm tot.l.), LECTOTYPE, *ex* West Coast of Africa, in good condition. NMV.4173

Br.St. 6, D iv 14, P i 14, V i 7, A iii 18, g.r. 130, scutes 18+12.

In percentages of standard length : body depth 39·4, body width 13·4, head length 34·0 ; snout length 8·3, eye diameter 7·5 ; upper jaw length 15·5, lower jaw length 18·0, post-orbital distance 18·7 ; pectoral fin length 21·8, pelvic fin length 12·7, length of anal fin base 17·9 ; pre-dorsal distance 49·2, pre-pelvic distance 56·2, pre-anal distance 76·5.

Body compressed, its width 3 times in its depth, the latter a little greater than head length ; belly keeled, but scutes lying in narrow groove formed by scales and thus scarcely projecting below profile of body. Head with adipose tissue covering much of upper part, adipose eyelid present and covering all but a third of eye. Cutaneous sensory canals on operculum, pre-operculum and 2nd sub-orbital and continued on scales behind occiput and around upper border of gill opening.

Snout a little longer than eye. Upper jaw with distinct median notch into which distal tip of lower jaw fits. Maxilla without longitudinal ridges, reaching posteriorly to vertical from just behind eye centre ; two supra-maxillae. No teeth in jaws or on tongue. Operculum with lower border rising steeply upwards ; anterior border of operculum with slight cut-away, exposing junction of sub- and inter-opercula.

Pseudobranch present, exposed, a little greater than snout length, the lower border forming a distinct ridge with a groove below it. Gillrakers as described in the neotype of *Clupea fimbriata* Bowdich (see Whitehead, 1967b : 591) ; longest rakers on lower arm of first arch equal to eye diameter and about three times length of corresponding filaments.

Dorsal fin origin nearer to snout than to caudal base by $\frac{3}{4}$ eye diameter ; first unbranched ray very small. Pectoral fin tip almost reaching to pelvic base ; one large and two small scales in axil of fin, forming a groove along $\frac{1}{2}$ length of fin. Pelvic fin base nearer to pectoral base than to anal origin by $\frac{1}{4}$ eye diameter. Anal fin origin nearer to pelvic base than to caudal base by $\frac{1}{2}$ eye diameter.

Scales adherent, about 40 in lateral series ; posterior edges fimbriated, as in Steindachner's figure (see Plate 2a).

Colour : uniform brown with dark brown at tips of anterior dorsal rays.

Identification. The genus *Ethmalosa* is monotypic and occurs only off the West Coast of Africa. The synonymy of the species is fully dealt with by Whitehead (1967b). The relationship of *Ethmalosa* to other genera of shads is discussed by Whitehead (1965b : 153).

10. ***Clupea notacanthoides*** Steindachner, 1869
= ***Ethmidium maculatum notacanthoides*** (Steindachner, 1869)

(Plate 2 b)

Alausa maculata Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 430 (Valparaiso—holotype redescribed by Whitehead, 1967a : 88).

Clupea notacanthoides Steindachner, 1869, *Sitzb. K. Akad. Wiss. Wien*, **60** : 309, pl. 7 (Mazatlan stated—probably erroneous) ; *Idem*, 1869, *Ichthyol. Notizen*, No. 9 : 20, pl. 7 (repeat).

Ethmidium chilcae Hildebrand, 1946, *Bull. U.S. natl. Mus.*, No. 189 : 82 (Callao and Chilka Bay, Peru).

Locality. No mention of Steindachner's species is made by Jordan (1895) in his list of fishes from Sinaloa, nor in the check-list of Jordan, Evermann & Clark (1930). In view of the mislabelling of the ' Mazatlan ' specimens of *Clupea setosa* (see p. 17), it seems probable that Steindachner's *Clupea notacanthoides* came from the normal range of *Ethmidium maculatum*, i.e. Peru or Chile.

Type material. Intensive search in Vienna has failed to produce the specimen(s) on which the description was made ; no size is stated, but the figure suggests a fish of about 175 mm S.L. (see Plate 2b).

Description. (based on Steindachner's description).

Br.St. 9, D 20, P 17, V 7, A 14, scales in lateral series *ca* 50, 7 predorsal scutes (? error for 17), ventral scutes *ca* 18+17.

In percentages of standard length : body depth 30, head length 32.

In percentages of head length : snout length 21, eye diameter 15·8, interorbital 25, lower jaw 55·5 ; longest dorsal ray 44·5, pectoral length 36·5 (57 in figure).

Dorsal origin $1\frac{1}{2}$ eye diameters nearer to snout than to caudal base. Pectoral falling short of pelvic base by just over 1 eye diameter (according to figure) ; a series

of enlarged scales above first ray. Pelvic base equidistant between tip of snout and caudal base. Anal base about one eye diameter shorter than head length ; longest ray 1¼ eye diameters.

Colour : a series of six black spots on the flank below the midlateral line.

IDENTIFICATION. The well illustrated dorsal scutes and high branchiostegal count confirm that Steindachner's specimen was a species of *Ethmidium*. Hildebrand (1946 : 84–85) proposed a new species, *Ethmidium chilcae*, for his Peruvian specimens, which he distinguished from *E. maculatum* of Chile in the following way.

	E. maculatum Lota, Chile (70–113 mm S.L.)	*E. chilcae* Callao & Chilka Bay, Peru (*ca* 100–212 mm S.L.)
Head in S.L.	3·25–3·4 (29·4–30·8%)	3·0–3·1 (32·3–33·3%)
Depth in S.L.	2·75–2·9 (34·5–36·4%)	2·8–3·1 (32·3–35·7%)
Caudal peduncle depth in head length	2·80–2·95	3·20–3·75
Pectoral fin tip short of pelvic base	by eye diam.	by pupil diam. or " less than eye " in adults
Ventral profile	more convex	
Scales	nearly smooth	denticulate

Examination of larger specimens from Chile (over 200 mm S.L.) shows that in adults the convexity of the belly profile, the denticulations on the posterior edge of the scale and the depth of the body reach the condition specified by Hildebrand for his Peruvian *E. chilcae* (e.g. in the type of *E. maculatum* from Valparaiso as redescribed in Whitehead, 1967a and in two British Museum specimens from the Gulf of Arauco, Chile). The only Peruvian specimen in the British Museum collection is a large adult, 245 mm S.L., which agrees with Hildebrand's diagnosis of *E. chilcae* in having a large head (35·8% of S.L.), a caudal peduncle depth 3·65 times in head length and denticulate scales. Unfortunately, the belly and pelvic fins are missing. Eight Peruvian specimens in the Copenhagen collections (*ex* Callao, 180–266 mm S.L., ZMC. 544–5 and 18289–91) agree with Hildebrand's diagnosis in head length (31·1–33·0% of S.L.), body depth (32·7–36·2% of S.L.), caudal peduncle depth in head length (3·07–3·75 times) and distance between pectoral tip and pelvic base (1¼–2¼ pupil diameters, but less than eye). The scales bear 20–22 denticulations on the posterior margin.

On the basis of the material examined and the small size of Hildebrand's Chilean specimens, it is likely that head length may distinguish Peruvian from Chilean stocks, but that body depth, scale form and apparent pectoral length are probably dependent on the size of the fish or on exogenous factors (trophic conditions).

Mann (1954) regarded Hildebrand's Peruvian material as a subspecies of *E. maculatum* and stated that it reached as far south as Antofagasta in Chile, its place then being taken by the nominate form. Two small British Museum specimens (82–92 mm S.L.) from Herradura Bay, just north of Antofagasta, clearly fit Hildebrand's diagnosis of *E. maculatum*. For the present, the two forms will be considered subspecies.

SYNONYMY. Hildebrand (*loc. cit.*) allied his *E. chilcae* most nearly to Steindachner's *Clupea notacanthoides*, but noticed slight differences in some proportions. Since it seems very likely that Steindachner had a Peruvian fish—and the description and figure suggest the large-headed Peruvian form—the slight differences noted by Hildebrand may well be attributable to faults in Steindachner's description, in which case the name *notacanthoides* should be used for the Peruvian subspecies.

Günther's type of *Clupea notacanthus* from Valparaiso (89·0 mm S.L., BMNH. 1848.6.14.42—one specimen now missing) is clearly the nominate form (head 30·6% of S.L.).

ILISHA Richardson, 1846

Ilisha Richardson, 1846, *Rept. Ichthyol. China Japan* : 306 (Type : *Ilisha abnormis* Richardson = *Alosa elongata* Bennett *fide* Whitehead, 1966).

Platygaster Swainson, 1838, *Nat. Hist. Animals*, **1** : 278 (Type : *Clupea africana* Bloch, designated by Swain, 1882, *Proc. Acad. nat. Sci. Philad.* : 280) ; *ibidem.*, 1839, **2** : 186, 294 (name preoccupied in Hymenoptera).

Zunasia Jordan & Metz, 1913, *Mem. Carnegie Mus.*, **6** (1) : 7 (Type : *Pristigaster chinensis* Basilewski = *Ilisha elongata*, see below).

Pseudochirocentrodon Miranda-Ribeiro 1923, *Comm. Linhas Telegr. Estrat. Matto Grosso Amazonas*, **58** : 8 (Type : *P. amazonicum* Mirando-Ribeiro).

Euplatygaster Fowler, 1934, *Proc. Acad. nat. Sci. Philad.*, **85** : 246 (Type : *Pellona brachysoma* Bleeker = *Ilisha indica*, see below).

At present, the genera *Ilisha* and *Pellona* are separated solely on the presence of a toothed hypo-maxilla in the latter (replacing the ligament connecting the tip of the pre-maxilla to the ventral edge of the maxilla). The presence of a toothed hypo-maxilla also separates the New World *Harengula* from the Indo-Pacific *Herklotsichthys* (subfamily Clupeinae), and the New World Pacific coast *Pliosteostoma* from the Atlantic coast *Odontognathus* (subfamily Pristigasterinae).

Having found a specimen of the *Ilisha-Pellona* complex with the hypo-maxilla present on one side and absent on the other, Myers (1950) preferred to await other evidence before splitting the genus *Ilisha*. Hildebrand (1964 : 415) also combined *Ilisha* and *Pellona*, but Berry (1964 : 729) split them again. No supporting evidence has yet been published, and I have been unable to find consistent differences in gill arches, fronto-parietal striation patterns, shapes of bones in the opercular and maxillary series, scutes or scales. Nevertheless, the separation of the species on a single, easily determined character (the hypo-maxilla) is useful and the generic level is preferred here.

It is unfortunate that the separation of *Pellona* from *Ilisha* does not coincide with a geographical separation. Most of the Indo-Pacific species are *Ilisha*, but *Pellona ditchella* Valenciennes has a hypo-maxilla ; conversely, most of the New World species are *Pellona*, but two species of *Ilisha* are recognized. I have been unable to find consistent differences between the groups of species from the two geographical areas.

The only comprehensive key to the species of *Ilisha* is that of Norman (1923). Subsequent keys are also unsatisfactory in view of re-examination of the type

material of Richardson, Bleeker, Valenciennes, Bloch and Steindachner (Whitehead, 1966 ; Whitehead *et al.*, 1966 ; Whitehead, 1967a; Whitehead, 1969b ; and the present study), coupled with the work of Myers (1950) and Hildebrand (1964). The following key is by no means definitive. It is intended as a summary of recent published and unpublished work ; there is still great need for a full revision of the Indo-Pacific species.

Key to species *Ilisha*

A. New World

1 Post-pelvic scutes 6–7, total scutes 25–26 ; gillrakers 19–22 ; pelvic base nearer to anal origin than to pectoral base ; Atlantic drainage (Amazon of Brazil, Peru) . . . . . 1. ***I. amazonica*** (Miranda-Ribeiro, 1923)

2 Post-pelvic scutes 12–14, total scutes 34–39 ; gillrakers 23–24 (and 11–12 on upper arch) ; pelvic base equidistant between anal origin and pectoral base or slightly nearer to the latter ; Pacific drainage and coasts (Costa Rica to Ecuador) . 2. ***I. furthii*** (Steindachner, 1875)

B. Eastern Atlantic

. . . . . 3. ***I. africana*** (Bloch, 1795)

C. Indo-Pacific

1 Anal origin in advance of or below middle of dorsal base ; pre-pelvic scutes 24–27 ; gillrakers 17–22 (Burma, Java, Borneo) . . . . 4. ***I. pristigastroides*** (Bleeker, 1852)

2 Anal origin below posterior half of dorsal base

a. Pre-pelvic scutes 22–27, post-pelvic 10–14 ; gillrakers 20–24

i Body deep, 37% of S.L. ; Borneo . . . 5. ***I. macrogaster*** Bleeker, 1866

ii Body depth moderate, 30–34% of S.L. ; India, Borneo . . . . . 6. ***I. filigera*** (Valenciennes, 1847)

iii Body slender, 24–28% of S.L. ; India to China. 7. ***I. elongata*** (Bennett, 1830)

b. Pre-pelvic scutes 18–20, post-pelvic 7–9

i Body depth 37–41% of S.L. ; gillrakers 23–28 ; India to Singapore . . . . . 8. ***I. indica*** (Swainson, 1839)

ii Body depth 32–34% of S.L. ; gillrakers 19–21 ; India to Singapore . . . . . 9. ***I. megaloptera*** (Swainson, 1839)

There appear to be 39 nominal species referable to the genus *Ilisha*. To summarize recent work, these nominal species are listed (alphabetically) in Table 2, each name preceded by a number which allocates it to a species in the key given above. Following each entry is a reference (in parenthesis) to works in which type material or synonymies are discussed. Major difficulties surround species groups 5–7 and 8–9, in which body depth is used to separate species. Intraspecific variation in body depth is very poorly documented. The slender *I. elongata* is fairly distinctive, but the *macrogaster-filigera* complex may prove to be a single species. Similarly, the *indica-megaloptera* complex may also comprise a polytypic species in which variations in body depth and gillraker numbers can be correlated with habitat (purely freshwater, marine and intermediates).

The Swainson names *megalopterus* and *indicus*, based respectively on *Jangarloo* and *Ditchoee* of Russell (1803 : pl. 191 and pl. 192—reproduced in Whitehead, 1967a : pl. 8a, b), must be provided with neotypes. Russell's figure of *Jangarloo* shows a fish with 17+11 (? 18+12) scutes, a combination not yet found in Indo-Pacific specimens ; the count is presumed to have been 18+9 (i.e. section 2b of the key

above). Russell's figure of *Ditchoee* closely resembles Bleeker's figure and holotype of *Ilisha brachysoma* (Whitehead, *et al.*, 1966 : 98, pl. 13 (1)—from figure in *Atlas*), except that Russell gave an anal count of only 37 (47 rays in the holotype of *brachysoma*, but only 40 in the type of *Pellona micropus*). Even if Russell miscounted, a variation of 7 rays is rather large and it may later prove necessary to separate *I. brachysoma* from *I. micropus* (i.e. *I. indica*).

11. ***Pellona furthii*** Steindachner, 1875
= ***Ilisha furthii*** (Steindachner, 1875)

Pellona furthii Steindachner, 1875, *Sitzb. K. Akad. Wiss. Wien*, **70** : 388 (Bay of Panama, to 11½ zoll in length, i.e. 299 mm) ; *Idem*, 1875, *Ichthyol. Beitr.*, No. 1 : 14 (repeat).

Type material

a. LECTOTYPE, a fish of 201 mm S.L. (*ca* 260 mm tot.l.—caudal tips broken) *ex* Panama Bay in 1874, NMV.1110 [jar labelled I 1253 Steind. don. (typ)].
b. PARALECTOTYPE, 1 fish, 215 mm S.L. (as above).
c. PARALECTOTYPES, 2 fishes, 200–217 mm S.L., NMV.1106 (otherwise as above).
d. PARALECTOTYPE, 1 fish, 210 mm S.L., NMV.1111 (otherwise as above).
e. PARALECTOTYPE, 1 fish, 212 mm S.L., NMV.1872 (otherwise as above).
f. PARALECTOTYPES, 2 fishes, 210–217 mm S.L., NMV.1114 (otherwise as above).

Another fish, 232 mm S.L., *ex* Panama in 1876 (NMV.1883) is not part of the type series.

Description. A fish, 201 mm S.L., 260 mm tot.l. (estimated, caudal tips damaged), LECTOTYPE, *ex* Panama Bay in 1874, in good condition apart from loss of caudal tips, NMV.1110.

Br.St. 6, D iv 13, P i 14, V i 5 (both), A iii 45, g.r. 11+23, scutes 22+13.

In percentages of standard length : body depth 36·4, body width 9·2, head length 24·7 ; snout length 6·8, eye diameter 8·0, upper jaw length 13·1, lower jaw length 13·3 ; length of pectoral fin 19·7, length of pelvic fin 6·4, length of anal fin base 45·0 ; pre-dorsal distance 45·7, pre-pelvic distance 43·4, pre-anal distance 60·0.

Body strongly compressed, its width 4 times in its depth, the latter 1½ times head length ; dorsal profile irregular, with slight " hump " behind occiput, ventral profile evenly convex, scutes prominent especially behind pelvic fin base.

Eye large, its diameter greater than snout length and 3 times in head length. Upper jaw reaching to just before vertical from eye centre ; median ⅓ of pre-maxillae toothless, a single series of minute conical teeth lateral to this ; no hypo-maxillae ; lower edge of maxillae with a series of fine teeth ; two supra-maxillae present, the 1st (anterior) slender and ½ eye diameter, the posterior with slender anterior shaft and expanded posterior part reaching almost to tip of maxilla (Figure 1). Lower jaw strongly projecting (7·5 mm beyond tip of snout), upper border rising, its height reaching half length of jaw just before midpoint ; a single series of 6–10 small conical teeth projecting inwards on either side of the symphysis.

Operculum with indentation along posterior border, its lower edge rising fairly steeply. Sub-operculum longer than deep, almost triangular. Entire gill opening covered by opercular series.

Pseudobranch present, exposed, a little under $\frac{1}{2}$ eye diameter in length, bearing about 25 filaments. Gillrakers slender, the longest $\frac{1}{2}$ eye diameter ; gill filaments of anterior and posterior hemibranchs subequal, the longest 2·8 times in eye diameter. Four stubby gillrakers on posterior face of 3rd epibranchial.

Granular teeth present on tongue, palatines and endo- and ectopterygoids ; no teeth on vomer.

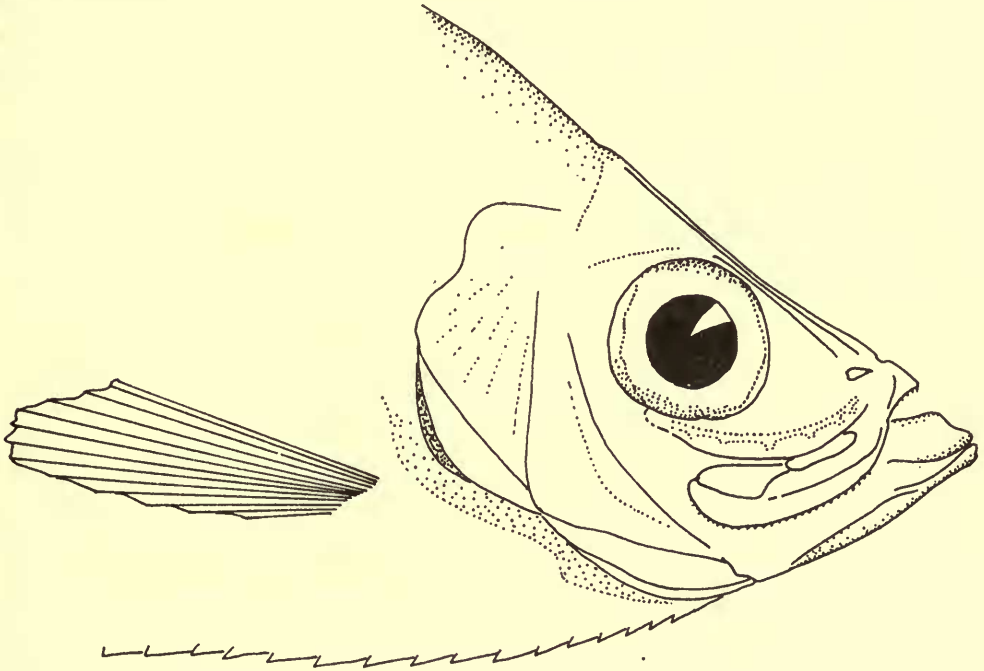

FIG. 1. *Pellona furthii* LECTOTYPE, 201 mm S.L., NMV.1110 (= *Ilisha furthii*).

Dorsal fin origin nearer to snout than to caudal base by 1 eye diameter ; the first unbranched ray short and barely apparent. Pectoral fin tip broken but probably reaching to half-way along pelvic ; axillary scale present, $2\frac{1}{4}$–$2\frac{1}{2}$ times in length of fin ; base of fin nearer to snout tip than to pelvic base by $\frac{1}{4}$ pupil diameter ; base of fin covered by scales. Pelvic fin base equidistant between pectoral base and anal origin ; no axillary scale present (? lost). Anal origin nearer to caudal base than to snout tip by 1 eye diameter.

Scales partly lost, posterior (exposed) border with faint signs of erosion and some small radiating striae (especially in posterior scales) ; unexposed portion of scales with up to eight convex striae, all interrupted at centre of scale except the most posterior.

Colour : upper 1/10 of body brown, remainder of flanks silvery ; tip of pectorals and tips of posterior dorsal rays speckled brown.

IDENTIFICATION. The absence of a toothed hypo-maxilla in *Pellona furthii* was not unexpected. Norman (1923a) originally placed this species in his genus *Neosteus* (= *Pellona*) implying the presence of this bone, but assigned it to *Ilisha* when he had examined material (Norman, 1923b). Hildebrand (1946 : 91, footnote) could find no hypo-maxilla in six specimens from the Gulf of Guayaquil and, recognizing Norman's separation of *Pellona* from *Ilisha* on this character, placed his specimens in *Ilisha*.

Following the synonymy put forward by Myers (1950 : *Ilisha iquitensis* and *I. apapae* synonyms of *Pseudochirocentrodon amazonicum*), Berry (1964 : 729) deduced that there is a single species of *Ilisha* in the Western Atlantic drainage area of South America, *Ilisha amazonica* (Miranda-Ribeiro). No Western Atlantic specimens of *Ilisha* are in the British Museum collections, but *I. amazonica* is clearly distinct from *I. furthii* of Pacific coasts according to the descriptions of Hildebrand (1948 and 1964 : 421) and Myers (1950). The differences are shown in the key given above (p. 21).

Scute and some gillraker counts were made on the following seven British Museum specimens and the results incorporated in the key, together with counts for the types of *P. panamensis* (see below).

a. 4 fishes, 160–201 mm S.L., *ex* Guayas River, Ecuador, BMNH.1938.11.18.1–4.

b. 3 fishes, 216–238 mm S.L., *ex* Panama, BMNH.1938.5.15.305–7.

12. ***Pellona panamensis*** Steindachner, 1875
= ***Ilisha furthii*** (Steindachner, 1875)

Pellona panamensis Steindachner, 1875, *Sitzb. K. Akad. Wiss. Wien*, **70** : 389 (Panama) ; *Idem*, 1875, *Ichthyol. Beitr.*, No. 1 : 15 (repeat).

TYPE MATERIAL. LECTOTYPE, a fish of 280 mm S.L. (365 mm tot.l.), *ex* Panama, NMV.1887 (labelled 1874–I/909– pt. a.).

PARALECTOTYPE, a fish of 265 mm S.L., *ex* Panama, NMV. 1890 (labelled 1874–I/909- pt.).

There is a third, non-typical, specimen of 258 mm S.L., *ex* Tumbez, coll. Stokm., NMV.1886.

DESCRIPTION. Two fishes, 280 and 265 mm S.L., LECTOTYPE and PARALECTOTYPE, *ex* Panama, in fair condition, caudal tips broken, many scales lost, occipital region dissected in paralectotype, NMV.1887 and 1890. (Figures for lectotype cited first).

Br.St. 5 (6), D iii 13 (14), P i 14 (14), V i 6 (6), A iii 49 (47), g.r. 11+24 (11+24), scutes 24+13 (23+13).

In percentages of standard length : body depth 32·6 (32·0), body width 8·7 (9·1), head length 26·0 (26·1) ; snout length 7·4 (6·9), eye diameter 7·4 (7·6), length of upper jaw 13·5 (13·1), length of lower jaw 14·2 (13·9) ; pectoral fin length 17·8 (16·7), pelvic fin length 5·9 (6·0), length of anal base 34·4(41·3) ; pre-dorsal distance 49·0 (48·7), pre-pelvic distance 46·0 (45·7), pre-anal distance 62·7 (63·7).

These two specimens differ from the type of *Ilisha furthii*, a smaller fish (201 mm S.L.), only in the more slender body (32·0–32·6 ; cf. 36·4), less convex belly profile,

slightly shorter pectoral fins (16·7–17·8 ; cf. 19·7) which do not reach the pelvic fin base, and shorter anal fin base (34·4–41·3 ; cf. 45·0). The latter is surprising, especially since the lectotype of *P. furthii* has fewer anal finrays, but there seems to be no justification for separating Steindachner's *P. panamensis*, as Norman (1923b) also concluded.

PELLONA Valenciennes, 1847

Pellona Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 300 (Type : *Pellona orbignyana* Val., designated by Gill, 1861, *Proc. Acad. nat. Sci. Philad.* : 38).

Neosteus Norman, 1923, *Ann. Mag. nat. Hist.* (9) **11** : 17 (Type : *Pellona ditchela* Valenciennes by subsequent designation of Norman, *Zool. Rec. Pisces* for 1923 : 25).

As in the case of *Ilisha*, the species of *Pellona* are very much in need of revision. The work of Hildebrand (1964) and examination of the status of the two Valenciennes species, *P. castelnaeana* and *P. flavipinnis* (Whitehead, 1967a : 106–110), can be summarized in the following key.

I Indo-Pacific area ; scutes 18–19+8 ; anal iii-iv 32–24 ; gillrakers on lower part of 1st arch 23–25 . . . . . 1. ***P. ditchela*** Val., 1847

II New World

A. Post-pelvic scutes 10–14 ; anal iii 32–37 . . . . . .

1. Gillrakers on lower part of 1st arch 12–14 (Amazon system) . . . . . 2. ***P. castelnaeana*** Val., 1847

2. Gillrakers on lower part of 1st arch 23–31 (as above but also from Surinam and Paraná) . . . . . 3. ***P. flavipinnis*** Val., 1837

B. Post-pelvic scutes 5–7 ; g.r. 23–25

1. Anal iii 33–39 (Atlantic coasts from Panama to southern Brazil) . . . . . 4. ***P. harroweri*** (Fowler, 1917)

2. Anal iii 42 (single specimen from Newport, Rhode Island) . . . . . 5. ***P. narragansetae*** (Fowler, 1911)

Pellona ditchela, the single Old World species, not only is inseparable from the New World species on any feature that could be regarded as of generic or subgeneric importance, but is so close to *Pellona harroweri* of Costa Rican and Brazilian waters that separation of the two is very difficult. Since the only pristigasterine linking these two regions is a species of *Ilisha* (*I. africana* of West Africa), it might be assumed that *Pellona ditchela* and *P. harroweri* are isolated relicts from a formerly much wider distribution of *Pellona*. Speciation in the Indo-Pacific may have been held back by competition from the more numerous species of *Ilisha*, whereas in the New World it is *Pellona* that appears to have speciated at the expense of *Ilisha*. The possibility cannot be ruled out that the combination of scute, anal finray and gillraker counts that characterizes *P. ditchela* and *P. harroweri* and distinguishes them from all other species may have been arrived at independently in the two species.

The use of gillraker numbers to separate *P. castelnaeana* (12–14) from *P. flavipinnis* (23–31) seems justified by the discontinuity shown in Table 3 and Figure 2. In an earlier paper (Whitehead, 1967a : 110) the low gillraker count in the smaller syntype of *P. castelnaeana* appeared to be the only exception to a general trend of reduction in number in larger fishes. Inclusion of the low gillraker counts found in three

specimens (220–275 mm S.L.) of *P. altamazonica* by Hildebrand (1964 : 418) and the high counts found in large fishes from the Guianas, however, suggests that there are two species, each with fairly constant numbers of gillrakers. A " slight " difference was found in the length of the pectoral axillary scale relative to fin length between the two species (Whitehead, 1967a : 110), but the relationship appears to be allometric and overlap occurs.

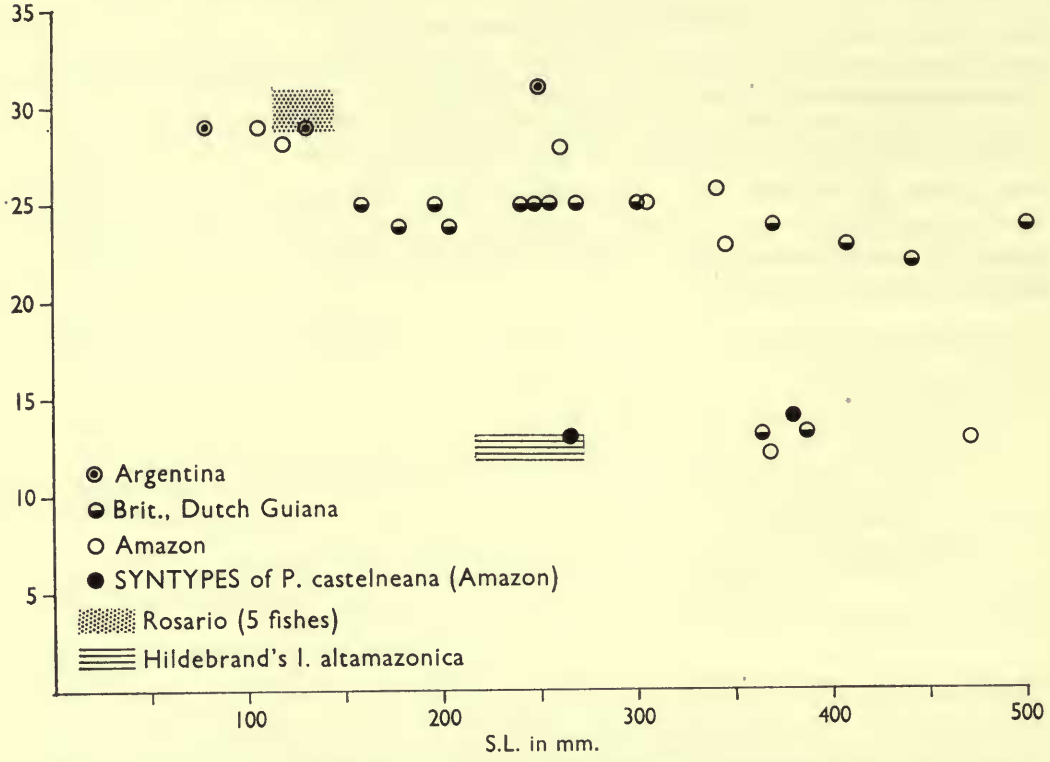

FIG. 2. Gillraker counts (lower arm, 1st arch) in specimens of *Pellona flavipinnis* (upper series) and *P. castelnaeana* (lower series). See Table 3, p. 44.

As Hildebrand (1964) supposed, *P. narragansetae* (known only from the holotype from Newport, Rhode Island, i.e. well outside the recorded range of the genus) was probably a stray and its separation from *P. harroweri* is perhaps not justified.

The following specimens have been labelled types of what appear to be MS. names never published by Steindachner.

" Pellona staudingeri "
= *Pellona flavipinnis* (Valenciennes, 1837)

A fish of 118·2 mm S.L., *ex* Iquitos (Peruvian Amazon), NMV.1112 (labelled 1884 I 300 a TYPE?).

A fish of 105·0 mm S.L., same locality, NMV.1893 (labelled I 1884 300).

The specimens have iii 34–iv 33 anal rays, 15+28 and 16+29 gillrakers, and 20+12 scutes. They are clearly *Pellona flavipinnis*, the high gillraker count distinguishing them from *P. castelnaeana* according to the key given here.

" Pellona macrolepis "
= *Pellona flavipinnis* (Valenciennes, 1837)

A fish of 340 mm S.L., *ex* Teffé (middle Amazon), NMV.1101 (labelled 1874—I, TYPE?).

This specimen has iii 37 anal rays, 14+26 gillrakers and 23+13 scutes. This high gillraker number reinforces the impression that there is no reduction in large fishes (Figure 2).

ODONTOGNATHUS Lacepède, 1800

Odontognathus Lacepède, 1800, *Hist. Nat. Poiss.*, **2** : 220 (Type : *Odontognathus mucronatus* Lacepède, 1800).
Gnathobolus Schneider, 1801, *Syst. Ichthyol. Blochii*, **2** : 556 (Type : *O. mucronatus* Lacepède).

Odontognathus is separated from the rather similar *Opisthopterus* Gill by its much longer maxilla (to gill opening or beyond ; cf. to vertical from eye centre in *Opisthopterus*). Berry (1964 : 729) showed that the maxilla exhibits positive allometry with standard length, and that in *Odontognathus* of 55–75 mm the elongation has already begun ; by 100–110 mm the tip of the maxilla has reached the opercular margin. Both genera lack pelvic fins but are otherwise similar to *Ilisha*.

Three species of *Odontognathus* are currently recognized and can be distinguished by the following key.

1 Scutes interrupted in area below pelvic fin base ; scutes with a single spine, outer margin not serrated ; anal rays 71–82 (Guianas to Trinidad) 1. ***O. mucronatus*** Lacepède, 1800
2 Scutes in continuous series ; outer margin of posterior scutes with 2–8 serrations
  a. Anal rays 58–62 ; scutes 25–27 ; dorsal origin over about 16th anal ray (Trinidad to Costa Rica). . . . . 2. ***O. compressus*** Hildebrand, 1923
  b. Anal rays 65–68 ; scutes 29–30 ; dorsal origin over about 25th anal ray (Pacific coast of Panama) . . . . 3. ***O. panamensis*** (Steindachner, 1876)

13. *Pristigaster (Odontognathus) panamensis* Steindachner, 1876
= *Odontognathus panamensis* (Steindachner, 1876)

Pristigaster (*Odontognathus*) *panamensis* Steindachner, 1876, *Sitzb. K. Akad. Wiss. Wien.*, **74** : 72 (Panama) ; *Idem*, 1876, *Ichthyol. Beitr.*, No. 5 : 24 (repeat).

TYPE MATERIAL. HOLOTYPE, a fish of 179·0 mm S.L., *ex* Panama, NMV.4626 (labelled 1874 I 2198 Steind. don.).

DESCRIPTION. A fish, 179·0 mm S.L. (204 mm tot.l., estimated), HOLOTYPE, *ex* Panama, in fair condition but tips of dorsal, anal and caudal fins damaged, scales mostly absent, NMV.4626.

Br. St. 4 (both), D i 11, P i 11, V (nil), A i 65, g.r. 8+20, scutes 30.

In percentages of standard length : body depth 25·3, body width 5·5, head length 17·3 ; snout length 4·6, eye diameter 4·8, upper jaw length 13·8, lower jaw length 8·0 (height 4·9) ; pectoral fin length 19·5, pelvic fin (absent), length of anal base 51·1 ; pre-dorsal distance 73·8, pre-anal distance 46·8.

Body strongly compressed, its width 5 times in its depth, dorsal profile "humped" at nape (? partly distorted) and concave over eye ; belly strongly keeled, scutes beginning on hind part of isthmus, prominent throughout, margins of 11th, 12th, 17th–30th scutes with 2–8 serrations (Figure 3b).

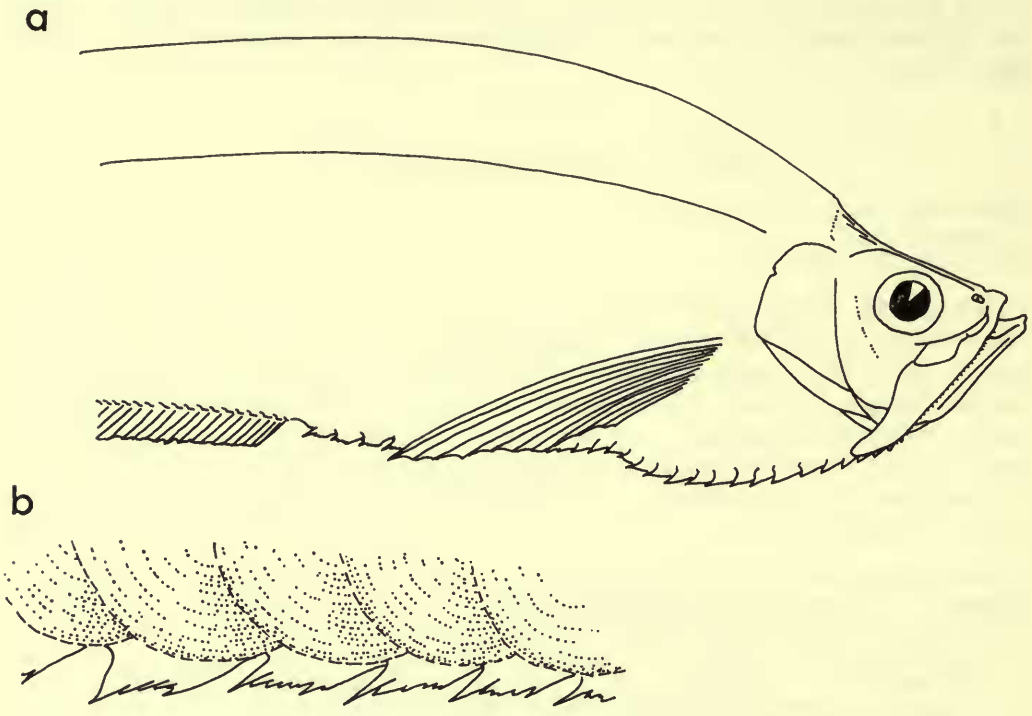

FIG. 3. *Pristigaster* (*Odontognathus*) *panamensis* HOLOTYPE, 179 mm S.L. NMV.4626 (= *Odontognathus panamensis*). *a*. Head and anterior half of body. *b*. Detail of serrated scutes behind pectoral fin tips.

Eye about equal to snout length, $3\frac{1}{2}$ times in head length. Upper jaw reaching to just beyond gill opening ; median $\frac{1}{4}$ of upper jaw edentulous, a single series of 10–12 fine, conical teeth on either side of this ; no hypo-maxilla ; lower edge of maxilla with a series of minute teeth reaching to posterior tip of bone ; two supra-maxillae present, the 1st (anterior) elongate kidney-shaped, 4·1 mm in length, the 2nd (posterior) with diamond-shaped expanded posterior part, 6·0 mm long and 3·9 mm deep, its posterior tip lying below vertical from eye centre ; maxilla depth rapidly decreasing behind tip of 2nd supra-maxilla, thereafter forming a slender blade (Figure 3a). Lower jaw slightly projecting, upper border rising rapidly, its height

reaching about ½ of jaw length in first third of jaw ; a single series of about 5–6 small conical teeth on either side of symphysis.

Operculum with lower border rising at about 45° ; sub-operculum twice as long as deep. Gill opening entirely covered by opercular series. No cleithral lobe.

Snout with strong, blade-like mid-dorsal ridge dividing before eyes and extending to hind end of skull ; two smaller ridges on either side, enclosing a canal ; a median ridge at hind end of skull and two faintly striated fronto-parietal triangular areas.

Pseudobranch present, exposed, with 10 filaments, its length 5·5 mm (⅔ eye diameter). Gillrakers slender, the longest 4·4 mm (⅞ eye diameter) ; gill filaments shorter, the longest 3·3 mm. Two stubby gillrakers present on posterior face of 3rd epibranchial (none on 2nd arch).

Granular teeth present on tongue, palatines, ecto- and endo-pterygoids, the toothed area becoming ridged posteriorly in the latter.

Dorsal fin origin above 25th branched anal ray, twice as near to caudal base as to posterior margin of pre-operculum ; dorsal rays damaged at tips, but apparently only a single, rather broad unbranched ray ; dorsal base short, ⅗ of eye diameter. Pectoral fin broad, its tip failing to reach anal origin by 2 eye diameters ; no axillary scale present. Pelvic fins absent. Anal fin base ½ standard length, anal origin nearer to snout than to caudal base by 1½ eye diameters.

Scales with slightly eroded posterior border and a few faint radiating striae ; unexposed portion without the main, uninterrupted vertical striation characteristic of clupeoid scales, but with 3–4 faint radiating striae not reaching centre of scale.

Colour : general light brown with two faint longitudinal silver lines, the first midlateral and the second a little above it ; cheek, operculum and belly silvery.

Identification. *Odontognathus panamensis* is very similar to *O. compressus* Hildebrand. Hildebrand (1923 : 194) found the dorsal origin slightly further forward in *O. compressus*, the anal fin base shorter and with fewer rays (58–62 ; cf. 65–68 in *O. panamensis*), and fewer ventral scutes (25–27 ; cf. 29). These are fairly small differences and a large sample of *O. panamensis* might bridge the discontinuity in finray and scute numbers. Both species have serrated scutes, which separates them from *O. mucronatus*, the latter further distinguished by a short non-scuted area below the pectoral fin base. *Odontognathus compressus* may yet prove to be merely an Atlantic subspecies of the Pacific *O. panamensis*.

Family **ENGRAULIDAE**

ANCHOVIELLA Fowler, 1911

Anchoviella Fowler, 1911, *Proc. Acad. nat. Sci. Philad.*, **63** : 211 (Type : *Engraulis perfasciatus* Poey).

Hildebrand (1943 : 108) redefined this genus to include species with a short and posteriorly rounded maxilla (Fowler had stressed the low number of gillrakers) ; Hildebrand recognized the subgenus *Amplova* Jordan & Seale for three species with exceptionally short maxillae, *A. balboae* (Jordan & Seale), *A. jamesi* (Jordan & Seale) and *A. brasiliensis* Hildebrand. Concentrating on maxilla length, Hildebrand failed

to recognize the nominal species *Stolephorus eurystole* Meek & Swain and *Anchoviella estanquae* Hildebrand as members of *Engraulis* (Whitehead, 1964b). *Anchoviella pallida* (Starks) belongs to another genus (see under *Anchovia*, p. 38), leaving 16 species of *Anchoviella*, distinguished mainly by rather small meristic and morphometric differences. In the majority of these species the number of gillrakers on the lower arm of the first arch is in the range 15–28 ; *A. balboae*, with 29–35, stands outside this range but examination of paratypical specimens of *Anchovia brevirostra* (= *A. balboae*) confirms this count and shows that this species is otherwise a fairly typical member of the *Amplova* group.

14. ***Engraulis vaillanti*** Steindachner, 1908
= ***Anchoviella vaillanti*** (Steindachner, 1908)

Engraulis vaillanti Steindachner, 1908, *Anz. Akad. Wiss. Wien*, **45** : 193 (Joazeiro and Barra on Rio São Francisco, Rio Grande do Norte, and Rio Preta, Brazil).

Type material.

a. LECTOTYPE, a fish of 62·7 mm S.L., *ex* Fazenda Ingaziera, labelled 1903 23/4b, NMV.1931.
b. PARALECTOTYPES, 15 fishes, 39–68 mm S.L., from the same jar.
c. PARALECTOTYPES, 16 fishes, 43·0–59·0 mm S.L., *ex* Lagao Viana, labelled 1903, MNV.1928.
d. PARALECTOTYPES, 6 fishes, 42·0–51·5 mm S.L., *ex* Lagao do Porto, labelled 1903 (¼)a, NMV.1929.
e. PARALECTOTYPES, 3 fishes, 42·9–45·0 mm S.L., *ex* Rio Preto, labelled 1903a, NMV.1930.
f. PARALECTOTYPES, 4 fishes, 39·2–42·0 mm S.L., *ex* Lagao Viana and Lagao do Porto, labelled 1903 31/3 ¼, NMV.1932.
g. PARALECTOTYPES, 2 fishes, 39·2–40·6 mm S.L., *ex* Lagao do Porto, labelled 1903c, NMV.1938.
h. PARALECTOTYPES, 4 fishes, juveniles of 25·0–37·2 mm S.L., *ex* Barinha, labelled 1903 17/3 b, NMV.1936.

Description. A fish, 62·7 mm S.L. (75·3 mm tot.l.), LECTOTYPE, *ex* Fazenda Ingaziera, in fair condition but scales mostly lost, lower caudal lobe broken, NMV. 1931.

Br.St. 12, D iii 10, P i 12, V i 6 (both), A iii 20, g.r. 14+19.

In percentages of standard length : body depth 21·2, body width 9·2, head length 26·3 ; snout length 5·1, eye diameter 7·1, length of upper jaw 20·5, length of lower jaw 16·7 ; pectoral fin length 16·7 (axillary scale 8·7), pelvic fin length 11·6 (axillary scale 4·7), length of anal fin base 23·5 ; pre-dorsal distance 54·5, pre-pelvic distance 45·5, pre-anal distance 65·8.

Body fairly compressed, its width 2·4 times in its depth, the latter less than head length. Snout moderately prominent, a little less than eye diameter. Width of head above eye a little less than eye diameter. Upper jaw just reaching to mandibular articulation but not quite to anterior border of pre-operculum ; tip of maxilla

evenly rounded, projecting only slightly beyond tip of 2nd (posterior) supra-maxilla ; the latter spatulate, tapering anteriorly and overlain half-way along its length by a plate-like 1st (anterior) supra-maxilla. Fine, close-set teeth on edge of maxillae, pre-maxillae and dentaries and minute teeth on palatines and ecto- and endopterygoids, but not on vomer.

Gillrakers fine, slender, the longest 2 mm long (about $\frac{1}{3}$ eye) and $1\frac{1}{4}$ times length of corresponding gill filaments ; 9 short rakers on posterior face of 3rd epibranchial. Pseudobranch present, exposed, about $\frac{1}{2}$ eye diameter. Isthmus brown (silvery in life?), sterno-hyoideus muscle not quite reaching to posterior border of branchiostegal membrane, the ventral edge of the urohyal exposed before this. A pair of crescentic posterior frontal fontanelles, together forming a triangle 1·6 mm long and 1·7 mm wide.

Dorsal fin origin equidistant between caudal base and posterior pupil border, i.e. nearer to caudal base by $1\frac{1}{2}$ eye diameters. Pectoral fin tips failing to reach pelvic base by $\frac{1}{5}$ eye diameter ; axillary scale present, almost $\frac{1}{2}$ length of fin. Pelvic fin base $\frac{2}{3}$ eye diameter before vertical from dorsal origin, nearer to pectoral base than to anal origin by $\frac{1}{2}$ eye diameter ; axillary scale present, $\frac{2}{3}$ length of fin ; inner rays of fins joined by membrane. Anal fin with low scaly sheath, its origin just behind vertical from last dorsal ray and $\frac{1}{2}$ eye diameter nearer to pectoral than to caudal bases.

Scales : unexposed portion with well-defined " shoulders " and 7–8 short horizontal striae, the two median striae meeting an irregular vertical striation ; exposed portion of scale with an irregular vertical striation followed by a reticular pattern of striae covering the rest of the posterior part of the scale ; hind border of scale not eroded. In some scales the reticular pattern extends forward and disrupts the (apparently) normal pattern of striae.

Colour : body brown with faint suggestion of silvery midlateral stripe ; a peppering of melanophores on snout, along entire dorsal profile, along posterior half of midlateral band (becoming heavier posteriorly) and on dorsal fin ; a dark vertical bar at base of caudal.

NOTE. Hildebrand (1943) had no specimens of *A. vaillanti*, but on the basis of Steindachner's description he distinguished the species by its high number of anal finrays, relatively few gillrakers and dorsal origin nearer to snout tip than to caudal base. As far as the lectotype is concerned, the latter is not true. Except for the posteriorly placed anal origin, *A. vaillanti* is close to *A. lepidenstole* (Fowler) but it has a more slender body. It also resembles *A. hubbsi* Hildebrand but has fewer gillrakers and a less prominent silver lateral band.

15. ***Engraulis nattereri*** Steindachner, 1879
= ***Anchoviella nattereri*** (Steindachner, 1879)

Engraulis nattereri Steindachner, 1879, *Sitzb. K. Akad. Wiss. Wien*, **80** : 174 (Pará, Brazil) ; *Idem*, 1879, *Ichthyol. Beitr.*, No. 8 : 56 (repeat).

TYPE MATERIAL. Intensive search failed to produce the type, a specimen of 50 mm. It may have been sent with duplicates to another museum.

DESCRIPTION. (based on Steindachner's description).

Br.St. (n.r.), D 12, P(n.r.), V (n.r.), A 28 or 29, g.r. (n.r.).

Snout fairly long, reaching well beyond tip of lower jaw, 4·0 in head ; eye larger than snout, 3·6 in head. Maxilla tip nearly square, not quite reaching to mandibular articulation. Gillrakers moderately long, longest equal to eye diameter.

Dorsal fin origin slightly nearer to base of caudal than to tip of snout. Pectoral fin a little longer than postorbital distance, its tip reaching half-way along pelvic fin. Anal fin origin below middle of dorsal base.

Colour : silver midlateral band indistinct.

NOTE. Maxilla shape, number of anal finrays and position of anal origin all strongly suggest a species of *Anchoviella*. Hildebrand (1943 : 133), who had no specimens and relied solely on Steindachner's description, kept this species distinct. The rather long pectoral fins suggest *A. pallida* (Starks), but with no record of gillraker number it seems best to follow Hildebrand for the moment.

ANCHOA Jordan & Evermann, 1927

Anchoa Jordan & Evermann, 1927, *Proc. Calif. Acad. Sci.*, (4) **16** (15) : 501 (Type : *Engraulis compressus* Girard).

This is the largest engraulid genus, with over thirty species recognized by Hildebrand (1943). The genus was originally distinguished from the very similar *Anchoviella* by the possession of more anal rays and gillrakers. Tables of anal ray and gillraker numbers given by Hildebrand (*loc. cit.*) show considerable overlap, however, and Hildebrand redefined the genus on the basis of the length of the maxilla :

Anchoa : tip of maxilla pointed, projecting well beyond tip of 2nd supra-maxilla and reaching beyond mandibular articulation, almost to gill opening.

Anchoviella : tip of maxilla truncate or bluntly rounded, projecting only slightly beyond tip of 2nd supra-maxilla and not reaching beyond mandibular articulation.

Three principal features distinguish both *Anchoa* and *Anchoviella* from *Engraulis* (Whitehead, 1964b ; summarized in Berry, 1964).

1. Posterior frontal fontanelles present (occluded in adult *Engraulis*).
2. Anal origin below or only just behind vertical from last dorsal ray (up to one eye diameter behind in *Engraulis*).
3. Pseudobranch short, equal to or less than eye diameter, not reaching to hyomandibular facet nor onto inner face of operculum, 15–25 pseudobranchial filaments (greater than eye, etc., 25–40 filaments in *Engraulis*).

Using these criteria, *Anchoviella eurystole* (Swain & Meek) and *A. estanquae* Hildebrand were recognized as members of *Engraulis* (Whitehead, 1964b : 882).

The redescription of the type of *Anchoa nasus* given below (p. 34) poses a further problem. In the three characters listed above, *A. nasus* approaches *Engraulis* while still maintaining the diagnostic feature of *Anchoa*, the long maxilla. The anal fin origin is not so far back as in *Engraulis*, the posterior frontal fontanelles appear to be excluded rather later in ontogeny and the pseudobranch is slightly shorter than

in *Engraulis*, but *A. nasus* is as close to *Engraulis* in these respects as it is to typical members of *Anchoa*. It has been noted (Whitehead, 1967a : 127) that three further species of *Anchoa* share these resemblances to *Engraulis, viz. A. lyolepis* (Evermann & Marsh), *A. argentivittata* (Regan) and *A. duodecim* (Cope) (B.M. specimens, including the type of *A. argentivittata*). Full revision of the anchovy genera may well support recognition of a separate genus or subgenus for these four species.

16. ***Engraulis januarius*** Steindachner, 1879
= ***Anchoa januaria*** (Steindachner, 1879)

Engraulis januarius Steindachner, 1879, *Stizb. K. Akad. Wiss. Wien*, **80** : 176 (*ex* harbour of Rio de Janeiro, Brazil) ; *Idem*, 1879, *Ichthyol. Beitr.*, No. 8 : 58 (repeat).

TYPE MATERIAL. LECTOTYPE, a fish of 51·4 mm S.L., *ex* Rio de Janeiro harbour, labelled " 1874 I 1566 ", NMV.2790.

PARALECTOTYPE, a fish of 54 mm S.L., from same jar.

DESCRIPTION. A fish, 51·4 mm S.L., LECTOTYPE, *ex* Rio de Janeiro harbour, in good condition, NMV.2790.

Br.St. 11, D iii 13, P i 12, V i 6, A iii 20, g.r. 21+27, scales *ca* 37 in lateral series.

In percentages of standard length : body depth 21·2, body width 7·8, head length 23·2 ; snout length 4·9, eye diameter 7·0, length of upper jaw 21·0, length of lower jaw 16·2 ; pectoral fin length 13·2, pelvic fin length 7·2, length of anal base 21·6 ; pre-dorsal distance 56·5, pre-pelvic distance 45·9, pre-anal distance 64·0.

Body compressed, its width 3 times in depth, the latter slightly less than head length. Snout a little shorter than eye diameter. Upper jaw reaching back beyond articulation of lower jaw and to vertical midway across pre-operculum ; lower edge of maxilla straight posteriorly, tip rounded, upper edge rounded to meet posterior tip of 2nd supra-maxilla ; the latter spatulate, tapering anteriorly ; anterior (1st) supra-maxilla slender, plate-like ; the maxilla projects 1·7 mm beyond the tip of the 2nd supra-maxilla. Teeth on pre-maxillae, maxillae and dentaries close-set, fine, very short ; fine teeth on palatines and ecto- and endo-pterygoids but not on vomer.

Gillrakers fine, slender, twice length of corresponding gill filaments and $\frac{3}{4}$ eye diameter ; 8 short rakers on posterior face of 3rd epibranchial. Pseudobranch present, partly invested in adipose tissue, with about ten short filaments, the length of the pseudobranch $\frac{1}{2}$ eye diameter. Isthmus silvery, sterno-hyoideus muscle extending forward almost to hind margin of branchiostegal membrane, the ventral edge of the urohyal exposed before this. Width of head over eye centre equal to eye diameter. A pair of triangular posterior frontal fontanelles, together 1·5 mm long and 1·4 mm at widest (posterior) point.

Dorsal fin origin equidistant between caudal base and posterior pupil border, i.e. nearer to caudal base than to snout tip by $1\frac{1}{3}$ eye diameters ; proximal half of fin invested in scaly sheath. Pectoral fin tips failing to reach pelvic base by $\frac{3}{4}$ eye diameter ; axillary scale present, $\frac{7}{10}$ length of fin. Pelvic fins small ; pelvic base $1\frac{1}{2}$ eye diameters before vertical from dorsal origin and equidistant between pectoral base and anal origin ; large axillary scale present (missing on right side), equal to fin

length. Anal fin origin below vertical from base of 8th branched dorsal ray and slightly nearer to caudal than to pectoral bases ; proximal half of fin invested in scaly sheath.

Scales : thin, apparently not caducous ; exposed portion with three complete irregular vertical striae, posterior edge slightly eroded ; unexposed portion with two short, incomplete vertical striae and two or three short radial striae from anterior edge of scale. The circulae on the unexposed portion of scale more widely spaced than those on the exposed portion ; the posterior $\frac{1}{3}$ of scale apparently without circulae.

Colour : body brown, with faint silvery midlateral stripe and silvery belly ; dark chromatophores forming diagonal line on upper part of caudal peduncle and a vertical bar below this.

NOTE. Hildebrand (1943) listed 36 species of *Anchoa*, for which he provided a complex and not altogether satisfactory key. Several species resemble *Anchoa januaria*, notably *A. mitchilli*, *A. parva*, *A. hepsetus*, *A. pectoralis* and *A. tricolor* (lectotype of the first fully described in Whitehead, 1967a : 127). Assessment of the importance of the small and mainly meristic differences separating these species must await full revision based on more material.

17. ***Engraulis nasus*** Kner & Steindachner, 1866
= ***Anchoa nasus*** (Kner & Steindachner, 1866)

(Plate 3a)

Engraulis nasus Kner & Steindachner, 1866, *Sitzb. K. Akad. Wiss. Wien*, **54** : 388, pl. 2 (17) (Chincha I., Peru).

Stolephorus cultratus Gilbert, 1892, *Proc. U.S. natl. Mus.*, **14** : 544 (Santa Margarita I., off Lower California).

SYNONYMY. Hildebrand (1943 : 70), who noted that the type of *Stolephorus cultratus* cannot now be found, allied that species with *Anchoa ischana* (Jordan & Gilbert) and *A. naso*. From Gilbert's description, however, *S. cultratus* is even closer to *Anchoa nasus*, differing only in minor respects (anal 20 ; cf. 21–27 ; maxilla " nearly to gill opening " ; cf. " not to margin of opercle "). Gilbert's species is perhaps a northern representative of *Anchoa nasus*.

TYPE MATERIAL. HOLOTYPE, a fish of 107·8 mm S.L., *ex* Chincha I., Peru, labelled Steindachner 1866 67, NMV.2837.

DESCRIPTION. A fish, 107·8 mm S.L. (132·6 mm tot.l.) HOLOTYPE, *ex* Chincha I., Peru, in good condition but scales mostly lost, NMV.2837.

Br.St. 13, D iii 13, P i 13, V i 6, A iii 20, g.r. 23+27.

In percentages of standard length : body depth 23·2, body width 8·9, head length 30·0 ; snout length 6·0, eye diameter 7·4, length of upper jaw 27·5, length of lower jaw 19·8 ; pectoral fin length 16·0 (axillary scale 9·5), pelvic fin length 10·2, length of anal base 22·6 (height of fin 12·2) ; pre-dorsal distance 56·2, pre-pelvic distance 45·8, pre-anal distance 69·0.

Body compressed, its width 2·6 times in its depth, the latter $\frac{3}{4}$ of head length.

Snout prominent, a little less than eye diameter. Upper jaw reaching back almost to hind margin of pre-operculum ; tip of maxilla pointed ; two supra-maxillae, the 2nd (posterior) spatulate, reaching to anterior margin of pre-operculum, the 1st (anterior) slender, plate-like ; maxilla projects 3·85 mm beyond tip of 2nd supra-maxilla. Anterior tip of lower jaw below vertical from anterior eye border. Teeth on entire lower edges of maxillae and on dentaries, fine and fairly close-set ; teeth on pre-maxillae even finer, granular teeth on palatines, ecto- and endo-pterygoids but not on vomer.

Gillrakers fine, slender, 1¼ times length of corresponding gill filaments and ⅔ eye diameter ; 9 short, stubby rakers on posterior face of 3rd epibranchial. Pseudo-branch present, fully exposed, its length 1½ eye diameters, about 30 filaments, the last two reaching onto the inner face of the operculum. Isthmus silvery, sterno-hyoideus muscle extending forward to posterior border of branchiostegal membrane, exposed portion of urohyal in front of this. Width of head over eye centre a little greater than eye diameter. Posterior frontal fontanelles occluded, the posterior tips of the frontals meeting in the midline and dividing only after reaching the supra-occipital ; frontal tips rounded posteriorly.

Dorsal fin origin equidistant between caudal base and posterior pupil border, i.e. nearer to caudal base than to snout tip by 1¾ eye diameters ; the few remaining scales suggest a scaly sheath to the base of the fin. Pectoral fin tips reaching ½ eye diameter beyond pelvic base ; axillary scale present, ⅓ length of fin. Pelvic fin base 1¼ eye diameters before vertical from dorsal origin, ½ eye diameter nearer to pectoral base than to anal origin ; inner rays joined to each other by a membrane, overlain by two elongate scales ; no axillary scale found. Anal origin nearer to caudal than to pectoral base by ½ eye diameter ; first unbranched anal ray a fraction behind vertical from base of last dorsal ray. Base of caudal with elongate scales reaching half-way along fin.

Scales : thin, many missing from anterior part of body but remainder firmly fixed ; anterior part of scale with distinct 'shoulders ' and 7 horizontal striae whose ends bend towards the centre of the scale ; exposed portion of scale with (usually) seven vertical pairs of striae, the first two short, the third bent posteriorly half way along their lengths, the fourth short, the fifth meeting in the centre of the scale and the remaining two curved and either short or continuous across the scale (in many scales, possibly regenerated scales, the striae are reticulate, more or less disrupting the apparently normal pattern of striation).

Colour : upper ⅓ of body light brown, remainder silvery, no sign of silver lateral stripe.

Note. The descriptions given by Hildebrand (1943) are insufficient to judge whether the resemblances of *A. nasus* to *A. ischana* and *A. naso* are superficial or whether they include the three features which *A. nasus* shares with *A. lyolepis*, *A. argentivittata* and *A. duodecim*, and which serve to distinguish these four species from all other members of *Anchoa* (see under genus, p. 32).

In the original description, the specimen was said to have a strongly convex dorsal profile and a nearly straight ventral profile (see Plate 3a). Hildebrand (1943 : 104) correctly assumed this to be a preservation artifact.

18. ***Engraulis peruanus*** Steindachner, 1879
= ***Anchoa nasus*** (Kner & Steindachner, 1866)

Engraulis peruanus Steindachner, 1879, *Sitzb. K. Akad. Wiss. Wien*, **80** (*ex* Callao, Peru) ; *Idem*, 1879, *Ichthyol. Beitr.*, No. 8 : 60 (repeat).

TYPE MATERIAL

a. LECTOTYPE, a fish of 100·0 mm S.L., *ex* Callao, labelled 1874 I 1215 (pt.a) Steind. don., NMV.1965.
b. PARALECTOTYPES, 3 fishes, 91·0–102·4 mm S.L., *ex* Callao, from same jar.
c. PARALECTOTYPE, 1 fish, 94·8 mm S.L., *ex* Callao, labelled as above but (pt.d), NMV.1966.
d. PARALECTOTYPES, 5 fishes, 79·3–97·6 mm S.L., *ex* Paraca Bay, as above, NMV.1964.
e. PARALECTOTYPES, 2 fishes, 86·4–89·4 mm S.L., *ex* Callao, as above but (pt.), NMV.1967.
f. PARALECTOTYPES, 2 fishes, 85·3–87·4 mm S.L., *ex* Callao, as above but (pt.c), NMV.1965.

DESCRIPTION. A fish, 100 mm S.L. (122·0 mm tot.l.), LECTOTYPE, *ex* Callao, in good condition but some scales lost, NMV. 1965.

Br.St. 13, D iii 13, P i 13, V i 6, A iii 23, g.r. 23+27.

In percentages of standard length : body depth 24·6, body width 8·3, head length 29·4 (width above eye centre 7·0) ; snout length 5·2, eye diameter 7·2, length of upper jaw 27·3, length of lower jaw 20·9 ; pectoral fin length 16·6 (axillary scale 9·8), pelvic fin length 10·0 (axillary scale 8·5), length of anal base 23·2 ; pre-dorsal distance 54·5, pre-pelvic distance 46·8, pre-anal distance 66·1.

In the remaining proportional and other features this specimen closely resembles the holotype of *Anchoa nasus* except that the anal fin origin is slightly further forward (below 11th branched dorsal ray ; cf. just behind last (13th) branched dorsal ray).

NOTE. Hildebrand (1943 : 102) placed *Engraulis peruanus* in the synonymy of *Anchoa nasus* on the basis of nine Steindachner specimens from Callao in the Museum of Comparative Zoology at Harvard. The description given here reinforces Hildebrand's view.

19. ***Engraulis panamensis*** Steindachner, 1875
= ***Anchoa panamensis*** (Steindachner, 1875)

Engraulis panamensis Steindachner, 1875, *Sitzb. K. Akad. Wiss. Wien*, **72** : 589 (*ex* Panama) ; *Idem*, 1875, *Ichthyol. Beitr.*, No. 4 : 39 (repeat).

TYPE MATERIAL

a. LECTOTYPE, a fish of 113·2 mm S.L., *ex* Panama, labelled 1874 I 1149 (pt.) Steind., NMV.1970.
b. PARALECTOTYPES, 2 fishes 112·7–125·0 mm S.L., *ex* Panama, from the same jar.

c. PARALECTOTYPES, 2 fishes, 113·6–113·8 mm S.L., *ex* Panama, as above, NMV.1969.
d. PARALECTOTYPES, 2 fishes, 109·2–114·9 mm S.L., *ex* Panama, as above, NMV.1972.
e. PARALECTOTYPES, 2 fishes, 91·2–97·5 mm S.L., *ex* Panama, as above, NMV.1971.

DESCRIPTION. A fish, 113·2 mm S.L. (139 mm tot.l., estimated, caudal tips broken), LECTOTYPE, *ex* Panama, in fair condition, NMV.1970.

Br.St.12, D iii 11, P i 13, V i 6, A iii 31, g.r. 18+22.

In percentages of standard length : body depth 27·4 (width 6·0), head length 22·8 (width over eye centre 6·1) ; snout length 3·5, eye diameter 6·6, length of upper jaw 20·7, length of lower jaw 15·8 ; pectoral fin length 20·2 (axillary scale 5·7), pelvic fin length 9·2, length of anal base 35·2 ; pre-dorsal distance 56·8, pre-pelvic distance 41·2, pre-anal distance 56·3 ; caudal peduncle, length 12·4, depth 10·2.

Body strongly compressed, its width 4·5 times in its depth, the latter greater than head length. Head rather deep and dorsally (snout to supra-occipital) rather short. Snout not strongly prominent, almost half eye diameter. Upper jaw reaching almost to gill opening (right maxilla tip bent downward, left maxilla tip possibly lacking final mm) ; tip of maxilla apparently sharply pointed, projecting well beyond 2nd (posterior) supra-maxilla, the latter spatulate and tapering anteriorly ; 1st (anterior) supra-maxilla plate-like. Symphysis of lower jaw slightly before vertical from anterior eye border. Teeth along entire lower edges of maxillae and on dentaries, fine and close set ; teeth on pre-maxillae very small ; granular teeth on palatines, ecto- and endo-pterygoids and a patch of 4 small teeth on either side of the vomer ; a line of granular teeth along upper edge of ceratohyal.

Gillrakers fine, slender, $\frac{3}{4}$ eye diameter and twice length of corresponding gill filaments ; 6 short rakers on posterior face of 3rd epibranchial. Pseudobranch present, exposed, $\frac{3}{4}$ eye diameter. Isthmus silvery, sterno-hyoideus muscle extending forward just to posterior margin of branchiostegal membrane, urohyal exposed before this. Posterior frontal fontanelles exposed, crescentic, separated anteriorly by a wedge, the fontanelles 1·8 mm long and together 2·2 mm wide.

Dorsal fin origin almost 2 eye diameters nearer to caudal base than to snout tip ; a low scaly sheath along base. Pectoral fin tips reaching beyond pelvic base by $\frac{2}{3}$ eye diameter ; axillary scale present, short, about $\frac{1}{3}$ length of fin. Pelvic fin base equidistant between pectoral base and anal origin ; axillary scale ?lost ; inner rays of fin joined by membrane to body and perhaps originally to each other. Anal origin equidistant between caudal base and posterior border of pupil and directly below vertical from dorsal origin ; low scaly sheath present. Caudal peduncle almost as deep as long.

Scales : oval, deeper than wide, not firmly fixed, many missing ; anterior part of scale with ill-defined radiating striae and a single irregular vertical striation traversing scale ; exposed portion with 2–3 pairs of short vertical striae followed by numerous fine vertical striae increasingly connected to each other posteriorly to form a network ; posterior margin of scale apparently eroded. In many instances this pattern is disrupted by extensive reticulation of the striae.

Colour : body light brown except for silvery lateral stripe a little wider than pupil diameter ; opercular series silvery.

NOTE. This species is well defined in the key and description given by Hildebrand (1943) except that in his specimens the silvery lateral band on the body was " nowhere much broader than pupil. "

The possession of vomerine teeth is not common in South American anchovies but occurs in some Indo-Pacific engraulids (e.g. *Thryssa*). The presence of denticulations along the upper edge of the ceratohyal, however, appears to be very rare in clupeoid fishes ; it is also found in large *Pterengraulis atherinoides* (135–190 mm S.L.—discrete tooth plates) and in *Anchoa spinifer* (over 70 mm S.L.—finely granular edge); in *Sardinops* there are numerous short plate-like but soft gillrakers.

ANCHOVIA Jordan & Evermann, 1896

Anchovia Jordan & Evermann, 1896, *Bull. U.S. natl. Mus.*, No. 47 (1) : 449 (Type : *Engraulis macrolepidotus* Kner & Steindachner).

This genus includes fishes which bear a strong resemblance to *Cetengraulis* (deep and compressed body, reduced jaw dentition and numerous close-set gillrakers which increase in number with size of fish). Members of *Cetengraulis* are clearly distinguished, however, by the broadly united branchiostegal membranes and the relatively long branchiostegal rays (about $\frac{1}{2}$ head length ; cf. $\frac{1}{3}$–$\frac{1}{4}$ in other engraulid genera).

A further reason for considering *Anchovia* close to *Cetengraulis* is that these two genera share a peculiarity that appears to be of some systematic importance in the clupeoid fishes, namely the absence of gillrakers on the posterior face of the 3rd epibranchial. First noticed by Dr. Carl Hubbs (*in litt.*) in the New World species of *Engraulis* (*E. ringens, E. mordax, E. anchoita* and *E. juruensis,* but not in *E. eurystole* and *E. estanquae,* which belong in *Engraulis sensu stricto*), the absence of these gillrakers is now confirmed in *Hildebrandichthys* as well as in the Indo-Pacific engraulid genus *Coilia.* These rakers are also absent in *Gilchristella aestuarius* and *Ehirava malabaricus* (subfamily Pellonulinae) and *Clupea* (*Strangomera*) *bentincki* (subfamily Clupeinae).

The genus *Anchovia* contains five species in which the maxilla tapers to a point and projects markedly beyond the 2nd supra-maxilla, namely *A. macrolepidota* (Kner & Steind.), *A. magdalenae* Hildebrand, *A. rastralis* (Gilbert & Pierson), *A. clupeoides* (Swainson) and *A. nigra* Schultz. Three further species closely resemble the above (posterior gillrakers of 3rd epibranchial absent, etc.), but have a blunt maxilla not reaching beyond the mandibular articulation and barely projecting beyond the tip of the 2nd supra-maxilla, namely *A. surinamensis* (Bleeker), *A. pallida* (Starks) and *A. potiana* Schultz & Menezes. Since maxilla shape is the principal distinction between the genera *Anchoa* and *Anchoviella,* revisionary work may well justify splitting the genus *Anchovia.*

20. ***Engraulis macrolepidotus*** Kner & Steindachner, 1865
= ***Anchovia macrolepidota*** (Kner & Steindachner, 1865)

(Plate 3b)

Engraulis macrolepidotus Kner & Steindachner, 1865, *Abh. K. Bayer Akad. Wiss.*, **10** : 21, pl. 3 (2) (Rio Bayano, Panama) ; Steindachner, 1876, *Sitzb. K. Akad. Wiss. Wien*, **72** : 587 (Panama).

TYPE MATERIAL

a. LECTOTYPE, a fish of 104·7 mm S.L., *ex* Panama, labelled 1876 II/1P, NMV.2808.
b. PARALECTOTYPE, a fish of 90·3 mm S.L., *ex* Panama, from the same jar.
c. PARALECTOTYPE, a fish of 136·6 mm S.L., *ex* Acapulco, Mexico, labelled 1874 I 1736 Kn. St., NMV.2807.

DESCRIPTION. A fish, 104·7 mm S.L. (129·2 mm tot.l.), LECTOTYPE, *ex* Panama, in fair condition but scales mostly lost, NMV.2808.

Br.St. 14, D iii 12, P i 14, V i 6, A iii 27, g.r. 108.

In percentages of standard length : body depth 31·7 (width 7·8), head length 29·7 ; snout length 3·9, eye diameter 6·8, length of upper jaw 26·4, length of lower jaw 20·4 ; pectoral fin length 15·1, pelvic fin length 7·5, length of anal base 28·4 ; pre-dorsal distance 54·2, pre-pelvic distance 45·1, pre-anal distance 59·5.

Body compressed, its width 4 times in its depth, the latter a little greater than head length. Snout fairly pointed, a little over half eye diameter ; width of head above eye centre less than eye diameter. Upper jaw reaching a little beyond mandibular articulation to posterior margin of pre-operculum ; tip of maxilla pointed, projecting 4·0 mm beyond tip of 2nd (posterior) supra-maxilla ; the latter spatulate, tapering evenly anteriorly and overlain about halfway along its length by the smaller 1st (anterior) supra-maxilla. Fine denticulations along edges of maxilla and mandible becoming fainter anteriorly and not present on pre-maxillae ; fine teeth present along edges of palatines and ecto- and endo-pterygoids, but not on vomer.

Gillrakers very fine and slender, the longest (7 mm) slightly exceeding eye diameter ; a double series of minute serrae along inner face of each raker ; no gillrakers present on posterior face of 3rd epibranchial. Gill filaments very short, 4½ times in length of gillrakers. Pseudobranch present, exposed, equal to eye diameter, bearing 24 filaments. Isthmus silvery, sterno-hyoideus muscle dividing halfway along to expose the ventral edge of the urohyal, the latter covered by silvery tissue until shortly before the hind margin of the branchiostegal membrane. A pair of exposed posterior frontal fontanelles, 1·4 mm in length, lateral borders forming a sigmoid curve.

Opercular series (Figure 4) not covering gill opening ; operculum inclined at an angle of 45° ; sub-operculum almost triangular, the junction of the posterior and ventral margins produced into a distinct point.

Dorsal fin origin nearer to snout tip than to caudal base by ½ eye diameter ; base of fin not invested in scaly sheath (? scales lost). Pectoral fin tips just reaching to pelvic fin base ; axillary scale present, ½ length of fin, bearing a narrow flange along lower edge ; pectoral fins set low on body, below level of sub-operculum. Pelvic fins small ; pelvic base 1 eye diameter before vertical from dorsal origin and equidis-

tant between base of pectoral and anal origin ; no axillary scale (? lost) ; final rays of fin joined together in midline by a membrane and also similarly joined to body. Anal fin origin below middle of dorsal base (7th branched dorsal ray) and 2 eye diameters closer to pectoral base than to caudal base ; base of fin invested in scaly sheath.

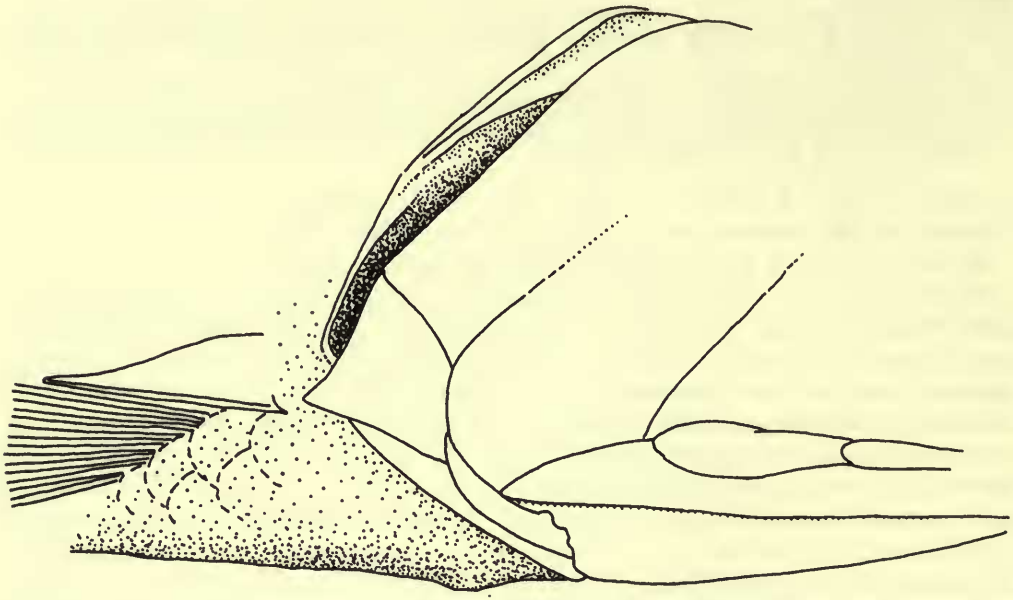

FIG. 4. *Engraulis macrolepidotus* LECTOTYPE, 104·7 mm S.L., NMV.2808 (= *Anchovia macrolepidota*). Opercular series (right side) showing characteristic shape of sub-operculum.

Scales : mostly missing ; exposed portion with an apparently random pattern of reticulated striae, unexposed portion with a single continuous curved striation preceded by up to five smaller radiating striae most of which fail to reach the centre of the scale.

Colour : upper ¼ of body brown, remainder silvery ; a dark line across bases of first few upper caudal rays ; very dark brown pigmentation on inner face of branchiostegal membrane.

LYCENGRAULIS Günther, 1868

Lycengraulis Günther, 1868, *Cat. Fish. Brit. Mus.*, **7** : 385 and 399 (Type : *Engraulis grossidens* Agassiz.

Hildebrand (1943) listed seven species of *Lycengraulis* and two further species have since been described, *L. limnichthys* Schultz and *L. simulator* De Plaza. In his key (p. 141), Hildebrand separated three species on the basis of their short, partly

rudimentary, gillrakers (*L. abbotti*, *L. barbouri* and *L. schroederi*). De Plaza (1962) noted a regression in the gillrakers of *L. simulator* with increasing size of fish but this did not reach the extreme condition found in the three species listed above. Hildebrand's specimens were all fairly large (148 and 205–237 mm S.L.), but he reported normal gillrakers in specimens of other species of a comparable size. It can be noted that small gillrakers are present on the posterior face of the third epibranchial in most species of *Lycengraulis* but are reduced or absent in specimens of *L. barbouri* at about 140 mm S.L. ; possibly this also occurs in the other species in which the gillrakers regress with age (*L. abbotti* and *L. schroederi*).

21. ***Engraulis poeyi*** Kner & Steindachner, 1865
= ***Lycengraulis poeyi*** (Kner & Steindachner, 1865)

(Plate 3c)

Engraulis poeyi Kner & Steindachner, 1865, *Abh. K. Bayer Akad. Wiss.*, **10** : 23, pl. 3, fig. 3 (Rio Bayano, Panama).

TYPE MATERIAL. Intensive search failed to produce any type material.

NOTE. *Lycengraulis poeyi* was well described by Hildebrand (1943 : 146), who placed it in the group with rather long and numerous gillrakers. It is the only member of the genus reported from the Pacific coasts of Central and South America ; it is well distinguished from the related *L. grossidens* and *L. olidus* of the Atlantic coasts by its high pectoral count (16–17 ; cf. 14–15), smaller jaw teeth and very short and blunt snout. Steindachner's description and figure (see Plate 3c) are adequate and the provision of a neotype is unnecessary at present.

TABLE 2

Alphabetical list of nominal species referable to the genus *Ilisha*. Numbers preceding name refer to senior synonyms listed in key (p. 21).

7. *abnormis* (*Ilisha*) Richardson, 1846, *Rept. Ichthyol. China Japan* : 306 (Whitehead, 1966 : 32).
7. *affinis* (*Clupea*) Gray, 1830, *Illustr. Ind. Zool.*, **1** : pl. 96 (2) (Whitehead, 1967a : 119).
3. *africana* (*Clupea*) Bloch, 1795, *Naturg. Aus. Fische*, **9** : 45, pl. 407 (Whitehead, 1969b : 268)
1. *amazonicum* (*Pseudochirocentrodon*) Miranda-Ribeiro, 1923, *Publ. Comm. Linhas Telegr. Estrat. Amazonas*, No. 58 : 8 (Myers, 1950 ; Hildebrand, 1964 : 241).
4. *amblyuropterus* (*Pellona*) Bleeker, 1852, *Verh. Bat. Gen.*, **24** : 21 (Whitehead *et al.*, 1966 : 94).
1. *apapae* (*Ilisha*) Hildebrand, 1948, *Smithson. misc. Coll.*, **110** (9) : 3, fig. 2 (Myers, 1950).
8. *brachysoma* (*Pellona*) Bleeker, 1852, *Verh. Bat. Gen.*, **24** : 22 (Whitehead *et al.*, 1966 : 100 ; Whitehead, 1967a : 116).
7. *chinensis* (*Pristigaster*) Basilewski, 1855, *Nouv. Mém. Soc. Nat., Moscow*, **10** : 243 (Fowler, 1941 : 662).
?8. *ditchoa* (*Pellona*) Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 313 (Whitehead, 1967a : 116).
3. *dolloi* (*Pristigaster*) Boulenger, 1902, *Proc. zool. Soc. London* : 271, pl. 30 (3) (Whitehead, 1967a : 112).
9. *dussumieri* (*Pellona*) Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 316, pl. 596 (Whitehead, 1967a : 113).
7. *elongata* (*Alosa*) Bennett, 1830, *Mem. Life of Raffles* : 691 (Whitehead, 1967a : 119).
6. *filigera* (*Pellona*) Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 322 (Whitehead 1967a : 117).
2. *furthii* (*Pellona*) Steindachner, 1875, *Sitzb. K. Akad. Wiss. Wien*, **70** : 388 (Hildebrand, 1946 : 91 ; see also p. 22).
3. *gabonica* (*Pellona*) Duméril, 1858, *Arch. Mus. Hist. nat.*, **10** : 259, pl. 3 (3) (Whitehead, 1967a : 112).
7. *grayana* (*Pellona*) Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 315 (Whitehead, 1967a : 119).
8. *indicus* (*Platygaster*) Swainson, 1839, *Nat. Hist. Anim.*, **2** : 294 (Whitehead, 1967a : 114, 117).
3. *iserti* (*Pellona*) Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 307 (Whitehead, 1967a : 112).
1. *iquitensis* (*Ilisha*) Nakashima, 1941, *Boll. Mus. Hist. Nat. "Javier Prado"*, **5** (16) : 66, fig. (Myers, 1950).
9. *kampeni* (*Pellona*) Weber & De Beaufort, 1913, *Fish. Indo-Austr. Arch.*, **2**: 87.
7. *leschenaulti* (*Pellona*) Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 311 (Whitehead, 1967a : 118).

5. *macrogaster* (*Ilisha*) Bleeker, 1866, *Ned. Tijdschr. Dierk.*, **3** : 300 (Whitehead *et al.*, 1966 : 98).
9. *macrophthalma* (*Platygaster*) Swainson, 1838, *Nat. Hist. Anim.*, **1** : 278 (*nomen oblitum*—Whitehead, 1967a : 115).
9. *megalopterus* (*Platygaster*) Swainson, 1839, *Nat. Hist. Anim.*, **2** : 294 (Whitehead *et al.*, 1966 : 103 ; Whitehead, 1967a : 114).
3. *melanota* (*Ilisha*) Derscheid, 1924, *Rev. Zool. Africaine, Bruxelles*, **12** : 278 (Whitehead, 1967a : 112).
8. *melastoma* (*Clupea*) Schneider, 1801, *Syst. Ich. Bloch.* : 427 (*nomen oblitum*—Whitehead, 1969b : 270).
8. *micropus* (*Pellona*) Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** ; 320 (Whitehead, 1967a : 116).
?8. *motius* (*Clupanodon*) Hamilton-Buchanan, 1822, *Fishes of Ganges* : 251, 383 (Whitehead, 1967a : 115).
7. *novacula* (*Pellona*) Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 319 (Whitehead, 1967a : 121).
2. *panamensis* (*Pellona*) Steindachner, 1875, *Sitzb. K. Akad. Wiss. Wien*, **70** (1) : 389 (see p. 24).
8. *parva* (*Platygaster*) Swainson, 1839, *Nat. Hist. Anim.*, **2** : 294 (on Gray, 1834, *Illustr. Ind. Zool.*, **2** : pl. 109 (3), *Clupea motius*).
4. *pristigastroides* (*Pellona*) Bleeker, 1852, *Verh. Bat. Gen.*, **24** : 20 (Whitehead *et al.*, 1966 : 93).
9. *russellii* (*Pellona*) Bleeker, 1852, *Nat. Tijdschr. Ned. Ind.*, **3** : 72 (Whitehead *et al.*, 1966 : 101).
7. *schlegelii* (*Pellona*) Bleeker, 1854, *Nat. Tijdschr. Ned. Ind.*, **6** : 418 (Whitehead *et al.*, 1966 : 99).
7. *sinensis* (*Pristigaster*) Sauvage, 1881, *Bull. Soc. Philom. Paris*, (7) **5** : 107 (Whitehead, 1967a : 119).
4. *sladeni* (*Pellona*) Day, 1869, *Proc. zool. Soc. London* : 623.
8. *verticalis* (*Platygaster*) Swainson, 1838, *Nat. Hist. Anim.*, **1** : 278 (Whitehead, 1967a : 116).
7. *vimbella* (*Pellona*) Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 317 (Whitehead, 1967a : 120).
6. *xanthopterus* (*Pellona*) Bleeker, 1851, *Nat. Tijdschr. Ned. Ind.*, **2** : 439 (Whitehead *et al.*, 1966 : 96).

TABLE 3

Gillraker counts in specimens of *Pellona castelnaeana* and *P. flavipinnis*.

	S.L.	gillrakers on lower arch
P. castelnaeana		
(Amazon basin)		
SYNTYPE MNHN.3705	380	14
SYNTYPE MNHN.3706	266	13
BMNH.1925.10.28.3	470	13
BMNH.1925.10.28.4	365	12
P. altamazonica (*fide* Hildebrand, 1964)	220–275	12–13
Guyana, Rupununi savannas.) BMNH.1969.7.17.98	363	13
P. flavipinnis		
(Amazon basin)		
BMNH.1897.7.17.19 (Amazon mouth)	345	23
NMV.1101 (Teffé)	340	26
BMNH.1929.11.18.2	305	25
BMNH.1869.5.21.51	260	28
NMV.112 (Iquitos, Peru)	118	28
	105	29
(Guyana, Surinam)		
BMNH.1934.9.12.2 (head only, 125 mm)	Approx. 500 mm	24
ZMA. (Marowijne R., Surinam)	438	23
	408	23
	370	25
BMNH. 1932.11.10.1	300	25
RMNH. (Surinam)	253	25
RMNH. 3344 (Surinam)	267	25
	248	25
BMNH. 1843.6.22.107	240	25
RMNH. 1675 (Surinam)	202	24
BMNH. 1936.5.6.1	197	25
BMNH. 1961.8.31.60	176	24
RMNH. (Surinam)	158	25
(Argentina) .		
BMNH.1965.9.8.28 (Rosario)	250	31
BMNH.1878.5.16.2 (Buenos Aires)	130	29
BMNH.1965.9.8.22–27 (Rosario)	114–145	29–31
BMNH. 1969.11.25.146	78	29

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PLATE 1

a. *Alausa alburnus* Kner & Steind. (= *Spratelloides delicatulus*)
b. *Pellonula bahiensis* Steind. (= *Rhinosardinia bahiensis*)
c. *Alausa fimbriata* Kner & Steind. (= *Sardinops sagax sagax*)

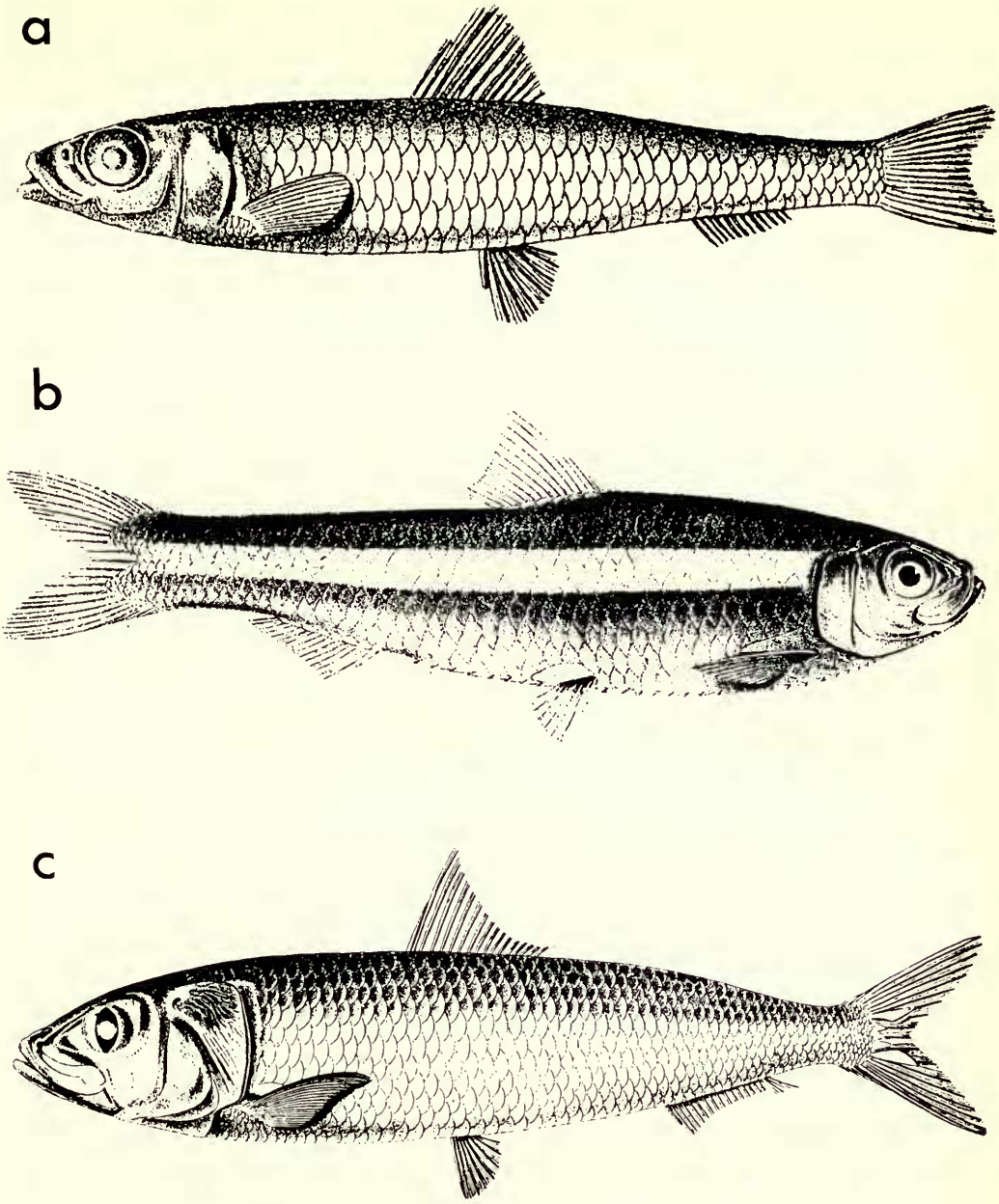
a
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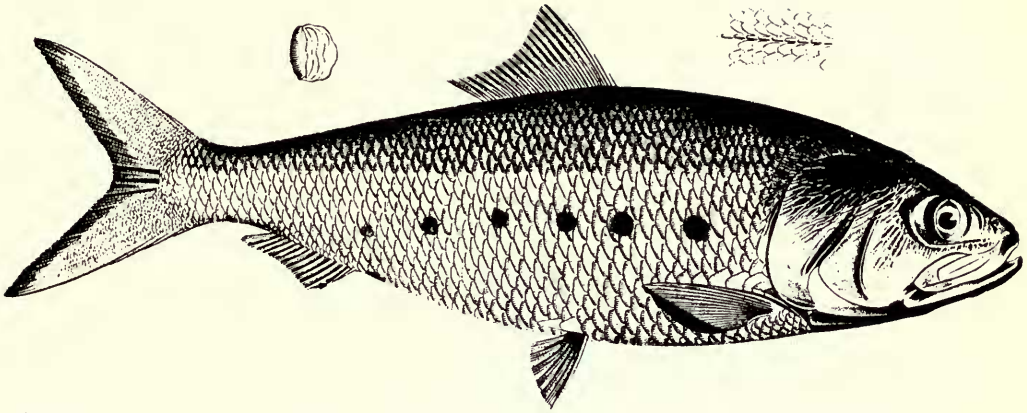
PLATE 2

a. *Clupea setosa* Steind. (= *Ethmalosa fimbriata*)
b. *Clupea notacanthoides* Steind. (= *Ethmidium maculatum notacanthoides*)

a



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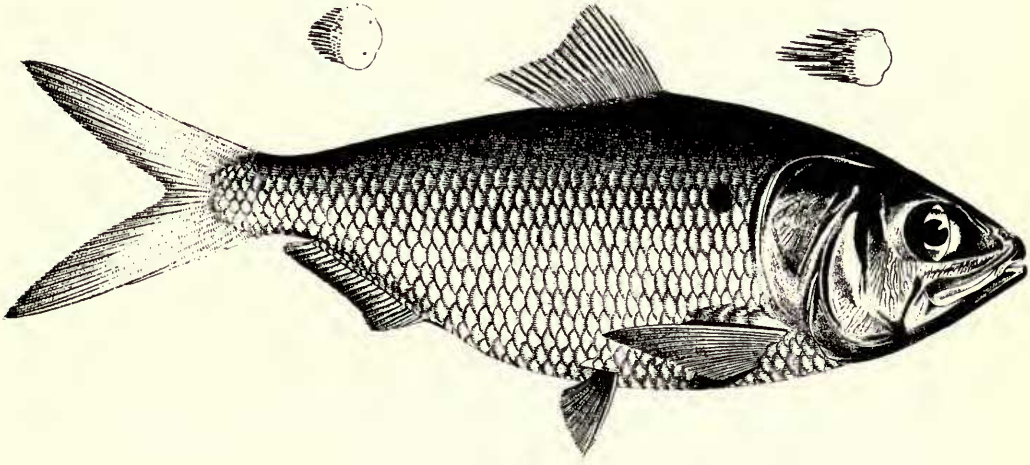
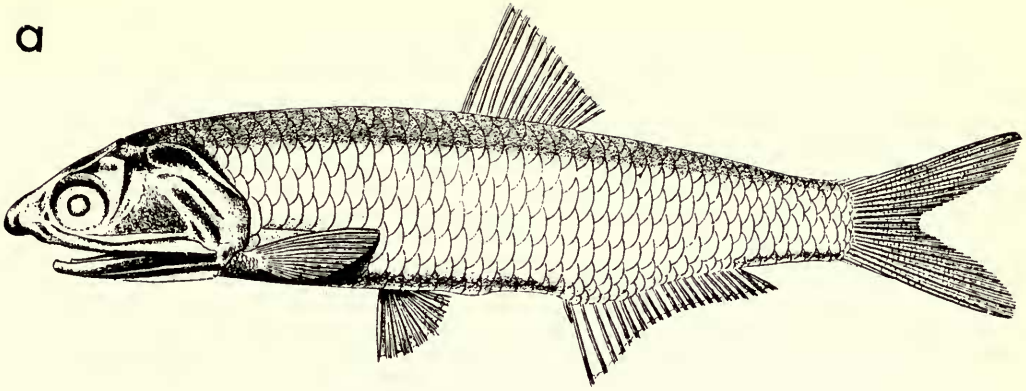


PLATE 3

a. *Engraulis nasus* Kner & Steind. (= *Anchoa nasus*)
b. *Engraulis macrolepidotus* Kner & Steind. (= *Anchovia macrolepidota*)
c. *Engraulis poeyi* Kner & Steind. (= *Lycengraulis poeyi*)

a



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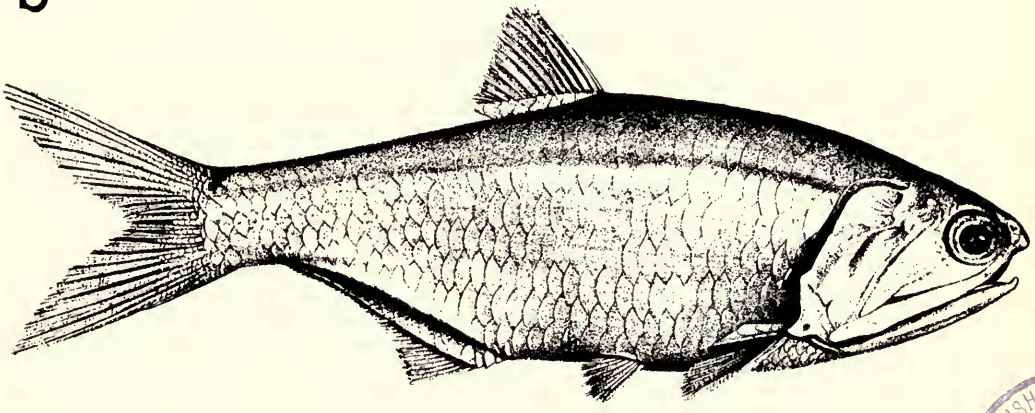

c